The American Midland Naturalist

Devoted to Natural History,

Primarily that of the Prairie States

Founded by J. A. Nieuwland, C. S. C.

CONTENTS

Environment of the Early Vertebrates—*Alfred S. Romer* and *Brandon H. Grove* 805

Summary of Upper Devonian Stratigraphy—*George H. Chadwick* ---- 857

The Aberrant Secondary Sex Characters of the Crayfishes of the Genus Cambarus—*C. L. Turner* ---- 863

The Anatomy of the Fresh Water Prosobranchiate Gastropod, Pleurocera Canaliculatum Undulatum (Say)—*Samuel R. Magruder* ---- 883

Studies on the Life History of a Snail of the Genus Lioplax—*Harley J. Van Cleave* and *Ray Chambers* ---- 913

Natrix Sipedon Sipedon in Central Indiana, its Individual and Sexual Variation—*Chapman Grant* ---- 921

Eggs and Young of the Pilot Black Snake and the Fox Snake—*Francis Harper* ---- 932

Birds of Dallas County, Texas—*Claude Kelley* ---- 936

A Study of the Relation of the Douglas Ground Squirrel to the Vegetation and other Ecological Factors in Western Oregon—*Elton R. Edge* ---- 949

The Abnormal Growth of the Molar Teeth and the Front Claws of an Adult Pocket Gopher, Geomys Bursarius (Shaw)—*Otis Wade* and *Paul T. Gilbert* ---- 960

Homonyms and Nomenclators—*Paul H. Oehser* ---- 962

Book Reviews ---- 965

Volume 16 **NOVEMBER, 1935** *Number 6*

EDITORIAL STAFF

THEODOR JUST,.....*Botany (Ecology, Taxonomy)*
Editor, University of Notre Dame

CARROLL LANE FENTON,.....*Invertebrate Paleontology*
West Liberty, Iowa

JOHN HOBART HOSKINS,.....*Botany (Morphology, Paleobotany)*
University of Cincinnati, Cincinnati, Ohio

REMINGTON KELLOGG,.....*Vertebrate Paleontology and Zoology*
U. S. National Museum, Washington, D. C.

MARCUS WARD LYON, JR.,.....*Mammalogy*
South Bend, Ind.

FRANCIS JOSEPH WENNINGER, C.S.C.,.....*Invertebrate Zoology*
University of Notre Dame

NOTE:—The AMERICAN MIDLAND NATURALIST, published from the biological laboratories of the University of Notre Dame, is primarily, though not exclusively devoted to the Natural History of the Middle West. A wide selection of papers on botany, geology, paleontology and zoology is published in bi-monthly issues, six of which make up a volume.

Fifty reprints will be furnished free of charge to contributors. Additional reprints should be ordered when proof is returned and may be had at cost price. Contributors will receive a free subscription for the year in which their paper appears.

The following numbers are out of print: vol. 2, 1, 2, 8, 10; vol. 3, 1-3, 7-9; vol. 4, 1-7; vol. 6, index, title page; vol. 10, index, title page; vol. 11, 1. All others available, 30 cents per copy. Complete volumes: $3.00; volumes 7, 13, and 14, $1.50 each; vol. 15 $2.00, single issues 35 cents; vol. 16 $3.00, single issues 50 cents.

Exchanges for journals, special volumes or duplicate books, and also specimens, should be arranged directly through the editorial office at the University of Notre Dame, where subscriptions also are received. Offers should accompany request for exchange.

For citation use this abbreviation: *Amer. Midl. Nat.*

Entered as second-class matter at Notre Dame, Indiana. Acceptance for mailing at special rate of postage provided for in section 1103, Act of October 3, 1917, authorized on July 3, 1918.

The American Midland Naturalist

PUBLISHED BI-MONTHLY BY THE UNIVERSITY OF NOTRE DAME, NOTRE DAME, INDIANA

VOL. 16 NOVEMBER, 1935 No. 6

ENVIRONMENT OF THE EARLY VERTEBRATES

ALFRED S. ROMER AND BRANDON H. GROVE

I. Introduction

The sea was long held to be the place of origin of the vertebrates, for their lower chordate relatives and most of the lower living fish types are ocean-dwellers. But certain theoretical considerations, and the fact that a number of finds of older fish types have been made in strata seemingly of non-marine origin, have led many to suggest the opposite: that the earliest vertebrates may have been inhabitants of fresh waters.

Relatively little has been done toward a resolution of this problem. Most vertebrate paleontologists who have dealt with fish material have been primarily interested in morphology and classification and offer little information concerning the conditions surrounding the funds, while the geologists, to whom we owe many of the discoveries of fish localities, have been mainly interested in stratigraphic rather than environmental problems. The only comprehensive treatment of the subject is that of the botanist J. M. MacFarlane in his "Evolution and Distribution of Fishes."[1] However, since this volume was written as an attempted corroboration of the autohr's previously reached conclusion that vertebrates originated in fresh waters from nemertean worms, it cannot be regarded as an unprejudiced study, despite the array of data cited, and the evidence in many cases seems to us to be used in quite an arbitrary fashion to support the author's beliefs.

In the present paper the writers have attempted to reach tentative conclusions regarding the environment of the early vertebrates in as objective a fashion as possible, through the study of the conditions under which the remains of a large series of early fishes have been deposited. We have made no attempt at a (necessary superficial) study of all fish finds, but have limited ourselves both chronologically and geographically.

We have considered only pre-Carboniferous records. In the Carboniferous, fishes were obviously dwellers in both inland and marine waters, the fresh water faunas including mainly higher bony types, the salt water forms consisting primarily of "sharks." The problem is which of the two environments then found is secondary; its solution is to be sought in the Devonian and earlier periods.

Since we are for the most part unfamiliar with European localities, we have limited ourselves to North American deposits, except for brief compar-

[1] New York, 1923.

isons. Some fifty formations of the United States and Canada contain pre-Carboniferous vertebrates. We hoped that these might furnish a representative sample of general world conditions, and this, we believe, has proved to be the case except in one respect that there are but few American equivalents to the Middle Old Red Sandstone fauna of Scotland, the Middle Devonian of America being dominantly marine in nature.

Little taxonomic or systematic revision has been attempted in our discussion of vertebrate types. In general we have accepted generic identifications as they exist in the literature, although many of these seem questionable. Species have been disregarded, genera being the smallest taxonomic units discussed. The literature of American fossil vertebrats is fully covered to 1928 in O. P. Hays's "Bibliography and Catalogue of Fossil Vertebrata of North America" [2] and in his "Second Bibliography",[3] and our references to literature are to the full citations to be found in that work except in the case of recent or purely geologic papers, which receive full citations here.

Certain problematical organisms have been omitted from our discussion. The recent flurry of interest in conodonts, due to their potential stratigraphic importance, has brought us no nearer to a solution of their zoological position, and no satisfactory interpretation of them as vertebrate remains has been forthcoming. Invertebrate paleontologists are inclined to class them as vertebrates, mainly on the ground that they do not fit into any known invertebrate group; but neither do they fit satisfactorily into any fish type—ostracoderm, lamprey, shark or higher bony fish. A "dawn fish" *Eoichthys* [4] has been described from the Middle Cambrian of Vermont on the basis of an impression of a single tiny plate. This Bather and others hold to be a fragment of a cystoid echinoderm.

In general our procedure has been to compile all the paleontological citations given in Hay's detailed and accurate bibliographies, and in connection with these to search out the related geological literature. Additional citations have been added by a review of the available literature of the last few years, not included in Hay's work.

In many cases where doubts have appeared as to the location, horizon or faunal and lithologic circumstances of the fish finds, we have consulted colleagues familiar with the formations concerned. In addition numerous friends have been kind have been kind enough to comment upon and criticize our discussions and conclusions. To all of these helpers and friendly critics we are deeply indebted for aid which has prevented us from making numerous factual errors, and from forming conclusions too precipitately. These friends include Dr. Carey Croneis and Curator A. W. Slocom of Walker Museum, Dr. C. L. Fenton, Curator S. K. Roy of the Field Museum, Dr. R. Ruedemann and Miss Winifred Goldring of the New York State Museum, Mr. G. H. Chadwick, Dr. G. A. Cooper of the United States National Museum, Drs. E. M. Kindle and L. S. Russell of the Canadian Geological Survey, Drs. P. E. Raymond and H. C. Stetson of Harvard University, and Dr. F. M. Swartz of Pennsylvania State College.

2 Bull. U. S. Geol. Survey **179**, 1902.
3 Publ. Carnegie Instn. **390**, 1929.
4 Bryant, 1926a.

We wish very particularly to express our thanks to Mr. G. H. Chadwick of Catskill, New York. As is now well known, the lateral changes in the various New York Upper Devonian formations have caused a chaotic situation in the nomenclature, and the numerous specimens of fossil fishes described from these beds by Eastman and others are difficult to place stratigraphically.[5]

We should have been unable to present any but the most garbled account of the New York Upper Devonian fishes without the unstinted aid of Mr. Chadwick, made possible not only by his knowledge of the stratigraphy of this region, but also through his intimate acquaintance with many of the vertebrate localities.

II. Criteria For the Determination of Environments

In attempting to determine the environment under which fossil fishes lived our evidence is, of course, mainly derived from a consideration of the associated fossils of other groups, and the nature of the enclosing sediments.

Paleontologic evidence.—The numerous and varied invertebrates characteristic of formations generally agreed to be marine in origin offer almost unquestioned proof of the saline nature of the water in which the beds containing them were deposited. The remains of marine animals may be carried a short distance into fresh waters by tidal currents or "tidal waves," but such exceptions need concern us but little.

As we turn to instances in which presumed marine types of invertebrates are present, but present in greatly reduced numbers and greatly decreased variety, the argument for a salt water origin of the sediments is vastly decreased. The presence of only a very few presumably salt water forms is highly suggestive of brackish water deltaic or estuarine conditions. If the same organisms are found repeatedly under these circumstances we may reasonably infer that we are dealing with forms which could withstand conditions of very low salinity. From their frequent presence in beds with a paucity of other invertebrates, the ceratiocarid crustaceans and members of the genera *Lingula* and *Leperditia*, for example, indicate this type of distribution.

In a considerable number of instances the older vertebrates are found in beds from which other fossil remains are entirely, or almost entirely, absent. Such conditions are strongly suggestive of fresh waters, in which invertebrates capable of fossilization are never numerous. Against this fresh water presumption two arguments may be brought: (1) considerable marine areas are today barren of invertebrate life, and such conditions were presumably present in the past; (2) in marine muds charged with carbondioxide, invertebrates may be numerous during life but their shells are rapidly destroyed by a solution of calcium carbonate, while phosphatic vertebrate remains are preserved.

These arguments show that in any single instance the absence of invertebrates does not positively indicate a fresh water origin for the containing sediments. But consideration of series of such instances leads to the belief that this argument for the widespread occurrence of barren marine sediments may readily be overworked, at least as regards vertebrate occurrences, and may lead

[5] In one instance the same specimen has been cited on three different pages of the same monograph as coming from three different formations.

to curious and untenable conclusions (cf. "Faunal contrast between groups," p. 46). Under the circumstances we feel that the absence of invertebrate fossils in fish localities gives a fair presumption of fresh water conditions. The Devonian black shales, which are involoved in the question of "sour muds," show faunas which in most respects are seemingly marine in nature. We have no strong reason to disagree, on grounds of fish distribution, with the suggestion that the paucity of invertebrate fossils in these beds is due to the solution of carbonaceous shells once present. We find puzzling the fact that in the case of the Cleveland shale, for example, remains are found not only of the bones and cartilages of fishes, but also exceedingly delicately preserved muscle fibres and kidney tubules. A selective solvent which would destroy most invertebrates without leaving the slightest trace, and yet conserve the most delicate of soft vertebrate tissues is difficult for us to imagine. Despite this we have almost universally accepted black shale localities as typically marine.

There are comparatively few Paleozoic forms of life from which positive evidence for fresh water conditions may be drawn. Terrestrial plant remains are, of course, important where found. Few pre-Carboniferous invertebrates are recognized as fresh water forms. Of these the most important are the eurypterids; O'Connell [6] has maintained that the eurypterids were in general fresh water dwellers.[7] In addition a few molluscs, such as *Amnigenia*, are generally regarded as fresh water forms On an earlier page we have noted the frequent presence of such forms as the ceratiocarids and *Leperditia* with fishes and eurypterids in otherwise barren beds. We suspect that certain species of these may well have been dwellers in inland waters as well as the seas.

Obviously, however, the presence of plants or other presumably fresh water or terrestrial organisms by no means conclusively proves the fresh water origin of the beds in which they are found, since such forms may readily pass downstream from fresh to brackish or salt waters before deposition takes place.

Evidence from sediments.—In the present status of our knowledge of sedimentation, indications of saline or non-saline conditions gained from the nature of fossil matrices are often suggestive but seldom conclusive. *A priori*, subsequent earth movements would tend to the preservation of marine Paleozoic sediments rather than those of continental type, but in the absence of positive proof of marine origin, evidence suggesting lagunal, deltaic, lacustrine or fluviatile origins is to be sought. Limestone deposits weigh the evidence heavily in favor of marine conditions, but a lacustrine origin is not impossible.[8] Sandstones are ubiquitous. Thick conglomerates are generally held to be of continental origin. Shales represent quiet bodies of water but may be

6 Bull. Buffalo Soc. Nat. Sci. **11**, no. 3, 1916.

7 Dr. Ruedemann informs us that in a paper now in press (Amer. J. Sci., 1934) he has been able to demonstrate the presence of marine invertebrates in certain of the supposedly fresh water eurypterid localities.

8 Dr. J. M. Weller, for example, informs us that his Pennsylvanian studies indicate the presence of limestones seemingly of fresh water origin covering considerable areas.

marine, estuarine, deltaic, lagoonal or lacustrine. Shales with a high content of carbon presumably derived from plant material indicate lagoonal conditions or quiet bodies of water near land; coal seams throw the balance strongly toward fresh water. Widespread uniformity of beds lends a strong presumption of marine conditions, although large lagoonal areas or lakes are presumably to be met with; channel walls suggest stream deposits, although they may represent brackish estuarine channels. The nature of the succession of beds may give us indication of the range of conditions in an area over a period of time, but cannot in itself fix the conditions in a particular layer containing vertebrate remains. Horizontal gradation of sediments and cross-bedding are generally indicative of deltaic or aeolian conditions. Mud-cracks, ripple marks and rain drop impressions indicate shallow waters exposed at times to the air, but without additional criteria may range from tidal flats to lake margins in their origins. Salt crystals indicate a shrinking inland body of water, but we know that such a body may have been either fresh or salt in its earlier history.

The provenience of the fossil remains.—For the sediments in which fossil aquatic vertebrates are found the burden of proof rests for the most part upon the shoulders of him who would claim them to be of continental origin. But our object is to ascertain the environment under which these fishes actually lived, not that under which they became deposited in sediments. The finding of a fossil vertebrate in marine strata by no means shows that this animal lived in a marine environment. The specific gravity of most fishes is very low, and a gas distended cadavar may float for a considerable time and a considerable distance before interment. If a deposit is of such a nature that currents were presumably negligible, the vertebrates discovered in it may be assumed to have lived in that region. Otherwise we may much more reasonably assume that they did not live where we found them, but in the region whence the currents came. The current may have been purely marine, the vertebrates living under conditions similar to those in which they were buried; but, especially in any area in which deltaic deposits are present, currents from river mouths and possible carriage of cadavers from the continents out into marine areas cannot be disregarded. Vertebrates from the upper reaches of streams would tend to be found, if at all, in their lower courses; low country stream dwellers would tend to be found prevalently in deltaic or estuarine deposits, or even in near shore formations of purely marine nature.[9]

The numbers and nature of the remains may afford a basis for judgment in many cases. Abundant well preserved cadavers are strong evidence for death at the place of deposition. Sparse remains suggest a "stray" from a distance, particularly if the form is one abundant elsewhere. Fragmentary

9 Kiaer, for example (1915a, p. 52), in his description of Devonian fishes from Ellesmere land, discusses the finding in one instance of "Old Red" fishes in association with marine or brackish mussels, and says: "there is, however, one point which I desire to emphasize. It is not proved that a fish has lived in a brackish water lake because we find its remains there — the river or rivers that flowed through such a region may have carried the body with it and deposited it in a different habitat. In such cases there will always be a certain amount of uncertainty."

remains may be due to the vicissitudes of lengthy transportation, but may also be laid to the animal's having been devoured by predators, or to wave action *in situ*.

In an attempt to determine the life environment of an aquatic form we are thus faced with two opposed bodies of knowledge. Positive evidence tends to throw the verdict as to the conditions under which any deposit was formed toward the marine side of the balance; considerations as to the probabilities of transportation after death tend to swing the balance in the opposite direction.

III. Ordovician

The oldest vertebrate remains reported from North America are from the Harding Sandstone of Colorado and related western formations. A fauna from the Harding quarry, near Canon City, Colorado, was described by Walcott.[10] The vertebrate material consists mainly of drift-worn bony plates and scales, always of a fragmentary nature. Three genera were discribed by Walcott—*Dictyorhabdus*, *Astraspis*, and *Eriptychius*. The first, as noted by Dean,[11] is probably not a vertebrate; the other two cannot be assigned definitely to any group, but are presumably ostracoderms of some sort. In addition Stetson [12] has described scales of the *Thelodus* type. The Harding [13] is a white saccharoidal sandstone of marine origin, in this region resting unconformably on pre-Cambrian strata, and overlain by a limestone containing an Ordovician fauna. The sandstone itself contains a number of genera of salt-water invertebrates.

> The lower bed is a shore-line deposit following the advance of the sea upon the land. . . The succeeding layers of the sandstones have more or less calcareous matter in the matrix. Their contained acephalous shells, drift-worn plates and scales of fishes, and the vast number of casts of annelid borings all prove the littoral nature of the sediments. . . The closing deposit of the sandstone series is formed of a coarse drifted sand, containing fragments of larger fish plates than those below. (Walcott).

Similar fragments have been found in beds seemingly of the same age near Ohio City, Colorado,[14] Gunnison, Colorado,[15] and in the Big Horn Mountains.[16] In the last instance the fish fragments are in the otherwise non-fossiliferous basal sandstone of the Bighorn Limestone, which is considered equivalent to the Harding Sandstone; limestones with marine invertebrates are present both above and below.

The littoral nature of the deposit [17] combined with the fragmentary nature

---

10 Walcott, 1892a.

11 Dean 1906b, p. 133.

12 J. Geol. **39**:152-153, 1931.

13 Cross, W., U. S. Geol. Survey, Pike's Peak Folio (1894); Darton, 1906a; Kirk, Amer. J. Sci. **20**(5):456-465, 1930; Behre and Johnson, ibid. **22**(5):477-486, 1933.

14 Cockerell, 1913a.

15 Cross, op. cit. (Note 13.)

16 Darton, op. cit. (Note 13.)

17 Drs. Raymond and Stetson inform us, however, that similar deposits are also to be met with today far off shore on the Atlantic continental shelf.

of the fossil material has led to the general acceptance of the theory that the Harding Sandstone vertebrates were in life inhabitants of fresh waters or, at the most, estuarine in habitat.

There is not the slightest trace of vertebrates in the abundant typical marine formations of the Ordovician.

European Ordovician—comparison.—In Europe, as in America, vertebrates are almost entirely lacking from the predominantly marine beds of the earlier Paleozoic. No vertebrates are recorded from the Cambrian, and from the Ordovician ("Lower Silurian") the only possible vertebrates are a few small tooth-like structures recorded by Rohon from the glauconitic sands of the Baltic.

IV. Silurian

Early Silurian of New York.—Specimens from the Shawangunk grit near Otisville, N. Y., which J. M. Clarke described as phyllocarid shells are believed by Bryant [18] to pertain to ostracoderms of the *Cyathaspis-Palaeaspis* type. These were found in thin black shale layers within the grit; the only other fossils are very abundant eurypterids,[19] and burrows *(Arthrophycus)*. These horizons seem clearly non-marine,[20] and C. K. and F. M. Swartz [21] have noted that the Shawangunk contains two distinct facies, one marine, the other Eurypterid bearing, the two interfingering.

Above the Shawangunk is the Guymard quartzite; here there are present two species of the ostracoderm *Cyathaspis*. No other fossils of any sort have been found. The quartzite is variegated in color, with gray, red, and olive, and in the upper part are thin layers of red shale in which are the vertebrate remains. This evidence suggests non-marine origin.

Niagaran of Pennsylvania.—In Perry County, Pennsylvania, the iron-bearing sandstone (Rose Hill) of the Clinton group contains a thin layer heavily charged with comminuted fish scales (perhaps *Palaeaspis)* and a spine referred to the "shark" genus *Onchus*.[22] No invertebrates are present here in this horizon; the iron-bearing sandstone in this area is generally barren, but contains occasional marine assemblages. From Perry County westward the Rose Hill as a whole appears to be marine in origin; to the east we "pass laterally into non-marine, possibly deltaic arenaceous beds. The iron sandstones of the Perry County area might be considered intermediate in character." [23]

Nerepis Hills, New Brunswick.—G. F. Matthew [24] described the ostra-

18 Bryant, 1926b, p. 260.

19 Clarke, N. Y. State Mus. Bull. **107**:301-303, 1907.

20 F. M. Swartz, *in litteris.*

21 Amer. J. Sci. **20**(5):667-674, 1930.

22 Claypole, 1884a, p. 1225; 1885d, p. 61; 2nd Penn. Geol. Survey Rept. Progress **F2**; xii, 9-94, 1885.

23 F. M. Swartz, *in litteris.*

24 1886a, 1887a, 1888a, 1907a; Bailey and Matthew, Geol. Survey Canada, Rept. Progress **1870**(1871):165.

coderms *Cyathaspis (Diplaspis)* and *Ctenopleuron*, and Stetson[25] has described scales referred to the ostracoderm *Thelodus* from a formation which Matthew believed to be of Clinton age, in the Nerepis Hills, New Brunswick. The vertebrate horizon consists of dark carbonaceous shales. Marine invertebrates are absent, but plant remains and numerous carapaces of a ceratiocarid are present. The evidence points strongly to a fresh water origin.

Moydart Formation, Nova Scotia.—A single fish tooth was described by Whiteaves[26] as having been collected some thirty years previously from the Upper Arisaig series at MacDonald's Brook, Nova Scotia. He considered the tooth as probably that of a crossopterygian which he provisionally named *Dendrodus arisaigensis*. The presence of a crossopterygian in these beds seems extremely dubious. Crossopterygians are common in beds of the "Old Red" type from the middle Devonian on, but only one rare genus is reported from the entire lower Devonian, and the present supposed find at such an early horizon is remarkable, if true. The beds here (Moydart Formation,[27] or possibly Stonehouse) consist of argillaceous limestones and shales of marine origin, bounded at the top by a "red stratum" of non-fossiliferous shales which may represent a brief recession of the sea.

This reputed occurrence is of too dubious a nature ot merit consideration.

Salina of Pennsylvania and Maryland.—Claypole[28] reports a thin bed of comminuted scales or shields, perhaps referable to *Palaeaspis*, in a 700 foot series of red shales in the Salina of Perry County, Pennsylvania. These "Onondaga red shales" are now called the Bloomsberg, and are barren of other fossils. This "is apparently a fluviatile-deltaic deposit which interfingers with lagoonal and marine deposits."[29]

At a higher horizon in Perry County Claypole and subsequent collectors have reported numerous specimens of the ostracoderm *Palaeaspis*, and *Onchus* spines in the Bloomfield sandstone. These are found in a bed of soft friable sandstone about ten feet in thickness, and of varying colors, dull red and greenish. No invertebrates are reported except the ostracod *Leperditia alta*. "The Bloomfield represents a marginal phase of the old Bloomsberg delta."[30] The evidence in general suggests an estuarine situation.

Palaeaspis is reported from the Tonoloway Formation in Maryland.[31] The locality or exact horizon of the find is not given. The Indian Springs Sandstone member, containing red beds and otherwise barren of fossils, is compared with the Bloomfield sandstone of Pennsylvania and quite probably is the source of the specimen listed.

---

25 Amer. J. Sci. **16**:233-235, 1928.

26 Whiteaves, 1898a.

27 Twenhofel, 1913a, pp. 300-301; McLearn, Canadian Geol. Survey, Mem. **137**:12-13, 1924.

28 Claypole, E. W., Geology of Perry County, Part I. Second Geol. Survey Penn., 1885, pp. 53-55; 1884a, 1884b, 1885a, 1885d; Bryant, 1926b, pp. 258-259.

29 F. M. Swartz, *in litteris*.

30 F. M. Swartz, *in litteris*.

31 C. K. Swartz, Maryland Geol. Survey. Silurian. p. 200, cf. pp. 46-47, 1923.

Silurian—Summary.—Vertebrates are reported from seven formations in the American Silurian. In six of the seven instances marine invertebrates are entirely absent, and the beds consist of red shales and sandstone or black shales. Although there are numerous Silurian marine horizons in which vertebrates might be expected to occur if present in salt waters, there is not a single instance of the presence of even a fragment of a vertebrate in a marine deposit, and the only association of a vertebrate with a possible marine fossil of any sort is the presence of the ostracod *Leperditia* in the Bloomfield. The evidence strongly indicates that Silurian vertebrates were predominantly fresh water forms.

European Silurian—Comparison.—As far as we are familiar with them, the European records show a similar situation. The majority of the Silurian vertebrate finds are from the Downtonian [32] of Great Britain, Norway and Spitzbergen; a much smaller number from the Ludlow and equivalents. Numerous "ostracoderms"—cephalaspids, pteraspids and anaspids—and spines of "Onchus" are found generally associated with many eurypterid remains, ceratiocaarids and an occasional *Beyrichia* or *Leperditia* but no other invertebrates. At Oesel, in the Baltic, vertebrates are found associated with very numerous eurypterids but seemingly not with a marine fauna, although marine invertebrates are found there at higher and lower levels. The closest approaches to marine conditions are seen in the occasional report of a pteraspid shell with brachiopods, the presumably estuarine conditions of the Ludlow bone-bed, and a very few fragments in the marine Upper Silurian of Bohemia. Despite the abundance of marine Silurian rocks, a marine vertebrate fauna is not present.

V. Lower Devonian

Knoydart Formation, Nova Scotia.—In the valley of McAras Brook in the Arisaig region of Nova Scotia is found the Knoydart Formation, containing a vertebrate fauna comparable to that of the Lower Old Red of Britain, including the ostracoderms *Pteraspis, Cephalaspis,* and *Psammosteus,* and isolated spines of *Onchus.* The formation [33] includes 683 feet of alternating red, green and brown argillaceous shales, flags, sandstones and traps; fish remains are found in six zones. Apart from eurypterid remains referred to *Pterygotus* no invertebrates have been found; there are a few plant remains, and some peculiar tracks. A thin section suggests a tufaceous origin. That these are fresh water beds is generally agreed. Ami suggested a lake deposit; Twenhofel believes it fluviatile.[34]

Campbellton Beds, New Brunswick.—On the banks of the Restigouche River near Campbellton Ells discovered a vertebrate fauna, described by Whit-

32 The Downtonian is considered by some to be properly Devonian rather than Silurian.

33 Ami, 1901b; Williams, H. S., Amer. J. Sci. **34**(4):244-250, 1912.

34 Twenhofel, 1913a, p. 303.

eaves,[35] Traquair,[36] and Smith Woodward.[37] The remains include abundant specimens of the ostracoderm *Cephalaspis* and of the primitive arthrodire *Phlyctaenaspis*, acanthodian shark fragments assigned to *Cheiracanthus*, *Climatius* ("*Ctenacanthus*") and *Acanthoessus* (*Acanthdoes*), small shark teeth described as *Protodus* and *Doliodus*, and the shark spines *Gyracanthus* and *Homacanthus*.

Invertebrates are rare, including only the eurypterid *Pterygotus*, a *Spirorbis* and minute *Valvata-like* gasteropods called *Cyclora*. Plant remains are fairly common; they were identified as *Psilophyton*, *Cordaites* and *Lepidodendron*.[38] The evidence is suggestive of a fresh water origin.

These beds are regarded by the Canadian Geological Survey as presumably equivalent to the basal beds of the Gaspé Sandstone, which is referred to the Middle Devonian. The fauna, however, seems highly comparable to that of the lower rather than the Middle "Old Red." The fish beds[39] rest on an eroded surface of tuffs of Lower Devonian age. The fossils occur in a dark gray massive argillite, including fragments of the underlying tuff, and overlain by massive sandstones, conglomeritic in places.

Nictaux Falls Region, Nova Scotia.—In a five-foot band of an ore, partly magnetite and partly hematite in composition, at Wheeler's Mine in this region has been found a fish spine referred to *Machaeracanthus*.[40] The formation contains a large marine invertebrate fauna, and is probably Oriskany in age.[41] Eastman[42] reports scales of *Thelodus* in the Oriskany Sandstone of this area. No details are given, and in default of them no interpretation can be attempted, although the Oriskany is generally marine.

Chapman Sandstone, Maine.—A bony plate referred by Eastman[43] to "*Asterolepis*" is described from the Chapman Sandstone (the plate is more probably of arthrodiran nature). The formation has been described by Williams[44] and Clarke,[45] and contains a good marine invertebrate fauna. The provenance of the single vertebrate specimen seems to be dubious, to say the least. It was contained in material shipped to Clarke, who apparently did not himself visit the area. He first states in text that it came from Presque Isle, and later lists it as coming from an outcrop at Edmunds Hill. If the fossil is actually from this formation it is presumably marine.

Bear Tooth Butte, Wyoming.—From this locality has come an interesting

35 Whiteaves, 1881e; 1889a.

36 Traquair, 1890a; 1893a.

37 Smith Woodward, 1892a.

38 Dawson, Can. Nat. **10**:8-11, 1883; Clarke, New York State Mus. Mem. **9**:87,90, 1908.

39 Whiteaves, 1881e, 1883b, and Drs. Kindle and Russell, *in litteris*.

40 Bailey, L. W., Can. Geol. Survey, Ann. Rept. (n. s.) **9**:102, 1896.

41 Dr. Raymond, *in litteris*.

42 1907b, p. 13.

43 1907b, pp. 40-41.

44 Williams, H. S., Bull. U. S. Geol. Survey **165**:78-88, 1900.

45 Clarke, N. Y. State Mus. Mem. **2**(2):93-128, 1909.

vertebrate fauna described by Bryant,[46] including abundant heterostracan ostracoderms—*Protaspis, Cryptaspis, Cardipeltis* and *Cyrtaspis,* the osteostracan ostracoderm *Cephalaspis,* the primitive arthrodires *Euryaspis* and *Anarthraspis,* five types of fish spines—*Onchus, Machaeracanthus, Pinnacanthus, Helenacanthus* and *Bulbacanthus*—and one tooth of the dipnoan *Dipterus*(?). The locality is described by Dorf.[47] The fish beds form a lens which appears to be a channel filling about 150 feet thick at the center, passing through the butte but disappearing laterally in less than 500 yards; it lies unconformably above an Ordovician limestone and below a chocolate-colored Devonian limestone (?Jefferson Dolomite). The material is shaly, red, gray, and yellow dolomitic limestone. Eurypterids are present, but no other invertebrate fossils of any sort. There are numerous plant remains, comparable to those at Campbellton. Dorf believes that the evidence indicates fluviatile to estuarine conditions, in fresh, or at the most, brackish waters.

Lower Devonian of Utah.—Branson and Mehl[48] have described a somewhat comparable fauna from Blacksmith Fork, Bear River Range, near Logan, Utah, including the pteraspids *Glossoidaspis* and *Cardipeltis,* the primitive arthrodire *Camptaspis* and fragmentary remains assigned to *Aspidichthys* but suggested by Bryant to pertain as well to one of the more primitive arthrodires. The remains were not found *in situ* but in blocks of talus presumably derived from the lowest zones of the thick Jefferson Dolomite. Although we understand that no invertebrate fauna is directly associated, the presence of these forms in a dolomite is strongly indicative of marine conditions.

Lower Devonian, Percé, Quebec.—A tooth of the lungfish *Dipterus* was found by Clarke[49] in a small Devonian area at Percé associated with marine invertebrates, including cup corals. Schuchert and Cooper[50] believe this deposit to be of Helderbgian age.

Lower Devonian—Summary.—The evidence from the American Lower Devonian suggests that, as in the Silurian, the center of vertebrate life lay in fresh waters, but that an epoch of transition had arrived. A comparatively small amount of vertebrate material has been collected from typical marine beds. Only at Blacksmith Fork is there a seemingly salt water vertebrate faunal assemblage, and here there are but a few types which are also found in contemporary fresh water deposits. Other marine finds include in all only three specimens—a Machaeracanthus spine, an arthrodire plate, and a lungfish tooth. On the other hand several good faunas, rich in specimens and containing a fair number of genera are reported in formations seemingly fluviatile or lacustrine in nature, in the Knoydart and Campbellton beds and at Bear Tooth Butte.

European Lower Devonian—Comparison.—In most respects our American

46 Bryant, W. L., Proc. Amer. Philos. Soc. **71**:225-254, 1932, and further papers in the same journal, 1933-34.

47 Bull. Geol. Soc. Amer. **44**:197, 1933; J. Geol. (in press, 1934).

48 J. Geol. **39**:509-531, 1933.

49 Thirteenth Int. Geol. Cong., Canada Guide Book **1**:85-110, 1913.

50 Amer. J. Sci. **20(5)**:171, 1930.

localities seem representative of conditions elsewhere, as indicated by European finds. The land phase is there abundantly represented by the lower "Old Red" (Caledonian) of Great Britain and Spitzbergen. Here are found many ostracoderms of the *Pteraspis* and *Cephalaspis* groups, *Thelodus*, numerous acanthodian sharks, *Protodus* teeth and, in Spitzbergen, numerous primitive arthrodires of the *Phlyctaenaspis* type; associated invertebrates include only numerous eurypterids and some myriapods; numerous plant remains are also present. These beds are a close parallel to the American localities in the Knoydart Formation, at Campbellton, and at Bear Tooth Butte.

For marine finds the Rhineland lower Devonian gives the best series.[51] The lower portion of the section there (Gedinnian) gives, in the Mondrepuits beds, a good marine invertebrate fauna, but no vertebrates; *Pteraspis* is present in the Gedinnian, but only in a higher, varicolored, barren formation, and there rarely.

In the later lower Devonian (Coblenzian) the Rhineland deposits give us the first European marine vertebrate assemblage, containing the elements present in marine rocks in America in the Lower Devonian and also forms showing an earlier stage of the marine fauna found in the Onondagan. As in the Oriskany, *Machaeracanthus* is present, as well as other shark species; as at Blacksmith's Fork, pteraspid ostracoderms and primitive arthrodires are found in marine waters; and in addition there are forms *(Gemündina, Epipetalichthys)* closely related to the armored "sharks" *(Asterosteus, Macropetalichthys)* of the Onondagan, and also rare fragmentary remains of a crossopterygian *(Porolepis)*.

VI. Middle Devonian

Columbus and Delaware Limestones, Ohio.—The Onondagan ("Corniferous") of Ohio contains the largest vertebrate fauna of Middle Devonian times. The armored sharks *Macropetalichthys* and *Onychodus* (an acanthodian?) are the commonest types. Arthrodires are frequent; besides *Acanthaspis*, a survivor of the primitive Lower Devonian type, there are more "normal" members of the group in *Coccosteus (Liognathus)*, a small *Dinichthys, Protitanichthys*, the ptyctodonts *Palaeomylus* and *Rhynchodus*, an early *pavement-toothed* shark, *Psammodus* (?), spines—*Machaeracanthus, Cyrtacanthus, Eczematolepis (Acantholepis)*, "scales" assigned (probably incorrectly) to *Coelolepis* and *Thelodus*,[52] one *Cladodus* tooth, the problematical "shark" braincase *Asterosteus* and the lungfish *Dipterus* (exceptional).

The Columbus is a limestone formation throughout; the overlaying Delaware is variable in nature, containing shaly layers and chert beds. Both are everywhere characterized by an extremely abundant invertebrate fauna. Fish remains are most plentiful in the uppermost six or eight inches of the Columbus, where there is a "bone-bed" of wide extent throughout the formation, containing innumerable fish fragments; but vertebrates are not confined to this horizon, and the marine association seems unmistakable.[53]

---

51 Gross (Abh. Preuss. Geol. Landesanst, N.F., Heft **154**, 1933) has recently summarized the Rhineland Devonian vertebrate material.

52 They appear from sections to resemble acanthodian scales (Stetson, *in litteris*).

Onandaga Limestone, New York.—In the Onondaga near Buffalo and Leroy, New York, a fish assemblage comparable to that of the Columbus and Delaware is present. Common forms include *Macropetalichthys, Onychodus, Acanthaspis,* indeterminate arthrodire plates, *Machaeracanthus, Cyrtacanthus* (?) and *Eczematolepis (Acantholepis, Oracanthus)*; additional genera include the arthrodires *Deinodus* and *Ptyctodus* (one specimen, fide Eastman).[54] The vertebrates are in intimate association with an extensive marine invertebrate fauna.[55]

Scattering Onondagan finds are reported from other localities in New York state. Eastman[56] lists *Coccosteus* from Clifton Springs, Ontario County. No details are given, but the usual marine conditions presumably hold. Eastman[57] also reports *Asterosteus* as possibly present in the Onondagan of New York. Spines of *Machaeracanthus* are reported from phosphatic nodules in Britton's Quarry and Manlius, Onondaga County, New York.[58] The deposit was originally considered Oriskany, but is Springvale (basal Onondagan); *Machaeracanthus* is not present in the Oriskany.[59]

Eastman[60] figures *Eczematolepis (Acantholepis)* from the "Ithaca" of Truxton, Cortland County, New York. This is an Upper Devonian area; Chadwick *(in litteris)* suggests that the fossil was probably found in Onondaga drift.

Onondagan of Ontario.—Macropetalichthys is reported from the Onondagan in several localities in southern Ontario, accompanying a good marine invertebrate fauna; these localities include Amherstburg,[61] Port Colbourne,[62] and Cargill;[63] at the first *Onychodus* is also present. *Machaeracanthus* is found at Walpole and Cayuga under similar conditions.[64] *Macropetalichthys* has been found in the James Bay region, in a limestone cliff associated with a number of marine invertebrates.

"Corniferous" of Indiana.—Norwood and Owen[65] described *Macropetalichthys* from the "Corniferous" of Indiana (Jeffersonville). The fish was found in a limestone containing numerous marine fossils, on Lewis Creek, 15 miles northwest of Madison, Jefferson County, Indiana. Newberry[66] states

53 Newberry, 1889, pp. 30, etc.; Stauffer, 1909a; Eastman, 1907b, pp. 61-62.

54 Hussakof and Bryant, 1919a, 8-10, 162; Eastman, 1907b, p. 70.

55 Luther, D. D., N. Y. State Mus. Bull. **99**:12-13, 1906.

56 Eastman, 1907b, p. 14, pl. 1.

57 Eastman, 1907a, p. 13.

58 B. Smith, 1910a, p. 658, and Bull. N. Y. State Mus. **281**:32-33, Fig. 14, 1929.

59 Chadwick, *in litteris.*

60 1907b, pl. 3.

61 Stauffer, Can. Geol. Surv., Mem. **34**:205, 1915.

62 Whiteaves, Can. Geol. Surv. Rept. Prog. **1875**:319, 1876; Stauffer, op. cit., pp. 27-37.

63 Stauffer, op. cit., pp. 149-152; Whiteaves, op. cit., pp. 316-320.

64 Whiteaves, op. cit., p. 319; Stauffer, op. cit., pp. 52-86, 149-152.

65 1846a.

66 1889a, p. 31.

that a bone-bed similar to that of the Ohio "Corniferous" and containing a similar fauna is present over a wide area in Indiana.

Hamilton Group, New York and Pennsylvania.—With the Hamilton we encounter the first of the thick black shale deposits which characterize a major portion of the later Devonian of western New York and the adjacent regions. In the succeeding discussion the majority of the localities yielding fossil vertebrates have been given a number in parenthesis; a corresponding number on the accompanying chart indicates the stratigraphic and horizontal position of the locality, and may assist in a better understanding of these relationships. We are indebted to Mr. Chadwick for his kindness both in drawing the chart and in acurately locating thereon the positions of the various vertebrate finds.

The Marcellus shale contains a marine invertebrate fauna. Vertebrates are described from a number of localities. Eastman [67] reports *Onychodus* in "enormous quantities" in the basal bituminous members (Union Springs) (2); Chadwick *(in litteris)* has found several teeth of *O. hopkinsi* in the Bakoven shale (basal Marcellus) at Webber Bridge (1), west of Catskill, New York. Specimens of *Dinichthys* have been described from the Marcellus near Syracuse (Cherry Valley Limestone) (3), the Livonia salt shaft (5), and Slate Rock Fall (6) near Geneva (Oatka Creek). [68] Shark denticles, perhaps of cladoselachians, are reported from the last formation at LeRoy [69] (4), and *Aspidichthys* and *Onychodus* are also present at Livonia. An acanthodian spine is noted from Onondaga Valley and unidentified acanthodian remains from Richfield.[70] *Onychodus* is listed as accompanying an abundant marine invertebrate fauna in Marcellus black shales at Stroudsburg, Pennsylvania.[71] Scales referred to either *Onychodus* or *Holoptychius* are reported from the Cardiff (?) of Oran (7), Onondaga County, New York.[72]

In the higher portions of the marine Hamilton there are several further vertebrate finds reported. *Dinichthys* is found at Haight's Quarry, Cazenovia (8),[73] (Skaneatles?), and *Aspidichthys* from East Bethany [74] (9) and Darien [75] (Ludlowville). Shark teeth referred to *"Diplodus" (Dittodus)* and "pustulose scales" (presumably some arthrodire) are found at Moscow (11) (Moscow shale), Geneseo, Livingston County, (Marcellus or Ludlowville) and East Bethany, Genesee County (Ludlowville).[76] *Machaeracanthus*

67 1907b, p. 169.

68 Claypole 1893f, pp. 276-277; Clarke 1894a, p. 161; Eastman 1907b, pp. 128-130; Smith, 1909b, 1910a.

69 Eastman, 1907b, pp. 17, 58, (not "Rhinestreet").

70 Smith, 1910a, pp. 662-663.

71 Willard and Cleaves, Bull. Geol. Soc. Amer. **44**:763-764, 1933.

72 Eastman, 1907b, pp. 15, 169, pl. 3.

73 Eastman, 1907b, p. 139.

74 Eastman, 1907b, p. 15.

75 Bryant, N. Y. State Mus. Bull. **281**:37-38, 1929.

76 Bradley, 1866a, pp. 70-72.

is present in the "trilobite bed" of the upper Ludlowville or Wanakah shale at Eighteen Mile Creek (10) on the shore of Lake Erie, in association in the very slab with several marine invertebrates.[77] *Ctenacanthus* is found associated with great numbers of marine invertebrates in the Moscow shales of Kashong Creek (12), Yates County,[78] and *Gamphacanthus (Heteracanthus)* is cited from the Moscow at Keeney.[79] *Gamphacanthus (Heteracanthus)* is also reported from the Hamilton of Canandaigua Lake[80] and *Gyracanthus* from the Hamilton of Madison County.[81]

The recent work of Chadwick and Cooper has shown that the red "Catskill" deposits of eastern New York state extend not only throughout the entire series of Upper Devonian deposits, but also extend downward into the Hamilton. Two "old red" deposits appear to lie in the Kiskaton beds, the type Catskill of Mather, and (as regards the vertebrate localities) an eastern extension of the Moscow horizon. At Gilboa, Schoharie County (13), Prosser[82] cites *Bothriolepis* in shales containing land plants but otherwise barren. Numerous fish remains (undescribed) were found during the construction of the New York City acqueduct. At Kaaterskill Creek, Palenville, New York (14), the same writer[83] lists *Coccosteus ("Dinichthys"), Sauripterus,* and *Holoptychius,* again from beds with land plants but otherwise barren. These citations from seemingly continental deposits give us the oldest records from continental North America of crossopterygians and antiarchs.[84]

Hamilton of Ontario.—Whiteaves[85] has described fragmentary material first identified as *Macropetalichthys,* later as *Aspidichthys,* from the Hamilton of Thedford, Ontario, and this same arthrodire is found at Arkona.[86] Both occurrences appear to be marine.

Traverse Series, Michigan.—Case[87] reports the arthrodires *Proditanichthys, Holonema, Dinomylostoma,* and *Ptyctodus,* and a spine identified as *Ctenacanthus,* from the Traverse. The remains are in a black limestone with many corals and stromatoporoids; the series is clearly marine. A tooth of *Dipterus* has been found by Curator A. W. Slocom of Walker Museum in a fossiliferous marine limestone in the upper part of the Traverse Series in Rose Quarry, Little Traverse Bay.[88]

77 Eastman, 1907b, pp. 85-86; Hussakof and Bryant, 1919a, p. 10.

76 Newberry, 1884b, p. 206, 1889a, p. 66.

79 Bryant, N. Y. State Mus. Bull. **281**:39-40, 1929.

80 Eastman, 1908a, p. 139.

81 Bryant, op. cit. (Note 79), pp. 38-39.

82 Rept. N. Y. State Geologist, **1897**:211, (1899).

83 Ibid., pp. 282-283 (1899) and Eastman, 1899f, p. 326.

84 On stratigraphic grounds the generic references of the Hamilton continental specimens seem doubtful. This fauna is worthy of further investigation.

85 1898b; cf. Stauffer, op. cit. (1915), pp. 173-176.

86 Stauffer, op. cit. (1915), pp. 168-172.

87 Contrib. Mus. Paleon. Univ. Mich. **3**: no. 9, 1931.

88 Winchell, The Grand Traverse Region: p. 45, section 862, Ann Arbor, 1866.

Middle Devonian of Missouri.—Fish remains are present in a number of Middle Devonian formations of Missouri described by Branson.[89] The Mineola Limestone is a crinoidal limestone with an abundant marine invertebrate fauna. *Dinichthys* (rare) and *Ptyctodus* (common) are present. *Dipterus, Onychodus,* and *Ptyctodus* are reported from the Calloway Limestone; the last a common form. All are found intimately associated with marine invertebrates. *Glyptaspis* and *Ptyctodus* are present in the next higher member, the Snyder Creek Shale, in zones containing numerous marine invertebrates. *Onychodus* is represented by two teeth in the Grand Tower Limestone of southeastern Missouri. No definite localitiy is mentioned, but the formation appears to be everywhere rich in marine invertebrates.

Jefferson Limestone, Montana, Utah.—Eastman [90] states that Kirk found a *Dipterus* tooth plate in the type section of the Jefferson Limestone on Gallatin River, near Logan, Montana. We have no further information regarding this (presumably marine) [91] occurrence. Branson and Mehl [92] report *Dinichthys* and *Ptyctodus* from a higher level of the Jefferson at Blacksmith's Fork, Utah, than that previously cited, under presumably marine conditions.

Gaspé Sandstone, Quebec.—The thick Gaspé Sandstone series has been studied by Logan [93] and by Clarke,[94] and is being redescribed by Alcock. In time it appears to cover a considerable portion of the Devonian. This series is composed mainly of sandstones alternating with shales of various colors, occasional conglomerates, and calcareous bands. Marine invertebrates are common at some horizons in sandy shales. In other layers plants are not uncommon but other fossils are rare, including only eurypterids, a *Lingula,* and a small *Modiomorpha* or *Carydium.* Conditions appear to range from fresh water to marine at various horizons. Vertebrates are present in two zones, *Cephalaspis* and *Machaeracanthus* in the plant containing shales of Logan's zone 1 and *Machaeracanthus* and *Onchus* [95] in zone 6, a conglomerate 156 feet thick of the type generally considered as continental in origin and containing some plant remains. The vertebrates thus appear to have been in all probability freshwater forms.

Middle Devonian, Ellesmere Land.—Kiaer [96] notes than in the "Fram" material from Ellesmere Land fishes were present in several Middle Devonian horizons. The only form preserved at the time of the description was a *Macropetalichthys* skull from the upper part of the marine "series D."

Middle Devonian, East Greenland.—Säve-Söderbeigh [97] has described

89 Branson, 1922a.

90 1917a, p. 246.

91 Cf. Kindle, Bull. Amer. Paleont. **4**: no. 20, 1908.

92 J. Geol., **39**:509-531, 1931.

93 Can. Geol. Surv., Rept. Progress **1863**:394-402.

94 Op. Cit. (1910), pp. 79-86.

95 Clarke reports *Ctenacanthus,* presumably in error.

96 1915a, pp. 8-16.

97 Nov. Act. Reg. Soc. Upsaliensis **9**:(4): 103-106, 1933.

remains of *Diplopterax (Diplopterus)* from an East Greenland locality of continental "old red" type and Middle Devonian age. The beds are similar in character to the Upper Devonian beds of the same general area described below.

Middle Devonian—Summary.—The Middle Devonian vertebrate record is in strong contrast to that of earlier times. In the Silurian and early Devonian the vertebrates, as recorded in North American deposits, appear to have been in great measure fluviatile forms; their remains are very seldom found in definitely marine environments. In the Middle Devonian, th Onondaga and Hamilton and equivalents, we find a well developed marine vertebrate fauna. Frsh water fishes on the other hand, are extremely uncommon finds; we have reported them only from the Middle Devonian "Catskill," Gaspé, and East Greenland. This does not by any means imply that fishes were actually rare in inland waters, but merely that continental deposits of this age are almost unknown in North America. Apart from the formations just mentioned there are practically no Middle Devonian formations which are not definitely marine in nature.

European Middle Devonian—Comparison.—While in Europe also Middle Devonian deposits are mainly marine, the middle "Old Red" (Orcadian) of northern Scotland and the Orkneys and Baltic "Old Red" beds give us a fair picture of Middle Devonian fresh water conditions. Especially abundant are the bony fishes, forms almost entirely absent in the Lower Devonian (crossopterygians are particularly numerus). The marine fauna is best known from the Rhine region, where a strikingly different fauna (there are but three common genera) is present. This marine assemblage is very similar to that of the Onandagan and Hamilton, with such ubiquitous forms as *Macropetalichthys, Onychodus, Rhynchodus,* and *Dinichthys.*

VII. Upper Devonian

In the Upper Devonian of New York and Northern Pennsylvania fossil fishes are present in numerous localities in various horizons and in all types of deposits, from those of unquestionably marine to those of unquestioned continental origins. We shall first consider the New York sequence in toto, and subsequently list the remaining Upper Devonian localities without particular regard to their stratigraphic position.

It has long been recognized that the lower and more westerly strata of the New York Upper Devonian (Genessee, "Portage," "Chemung") are characteristically marine, the higher and more easterly beds ("Oneonta," "Catskill") characteristically continental in nature, the continental beds forming a delta deposit of immense thickness. Despite the fact that changes in the nature of the sediments are to be expected in tracing any set of strata from west to east, it is obvious that many mistakes in correlation have occurred, and the literature on fossil fishes of this area is confusing and full of contradictions. We had found it impossible to give any coherent account of the fishes of the Upper Devonian of this area on the basis of the older literature. Chadwick's recent revision of the stratigraphy, however, has clarified the situ-

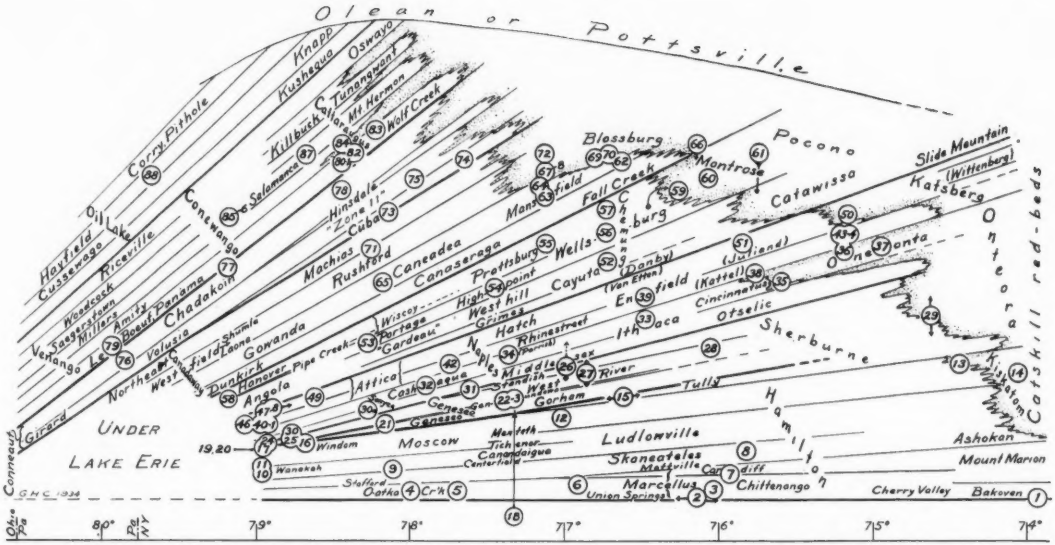


Fig. 1. Chart showing formations and fish localities in the Upper Devonian. The horizontal spacing of the chart is accurate to all localities where the data suffice. It has no vertical scale, and merely *suggests* that the formations thin to the west. The true thinning is so much greater that discrimination and labeling of formations to the west would be impossible if a true scale were used. Arrows have been added to the circles enclosing the locality numbers to show horizontal "spread" in cases in which the exact locality is doubtful, and vertical spread where there is uncertainty as to the precise stratic level. The contact of continental and marine formations is indicated by stippling within the margins of the terrestrial formations. (Chart by George H. Chadwick, 1934.)

ation, and we have unreservedly adopted his terminology for the New York and Pennsylvania fish localities. We have been very greatly aided by him in settling many problems regarding the localities, horizons and environmental conditions of various fossil fish finds. The majority of the fish localities of the Upper Devonian of New York and Pennsylvania have again been numbered in parenthesis to correspond with the locality number on Chadwick's accompanying chart, and their inter-relationships may thus be very simply presented.

Genesee Group (Senecan Series).—The Genesee, as is the case with all the major Upper Devonian divisions in New York, grades from marine beds (mainly black shales) in the west to continental beds in the east. But whereas the higher groups all include faunas of continental type, the Genesee finds are almost all from the western, marine portion of the section.

Eastman[98] mentions an undetermined "fin-spine" from the Tully Limestone at Cayuga Lake (15) New York.

The ptyctodonts *Ptyctodus* and *Palaeomylus* and teeth doubtfully referred to the pleuracanth genus *Dittodus* are found in the Geneseo ("Tully") pyrite horizon on Cazenovia Creek (16), near Springbrook, New York. This is the basal member of the black Geneseo shale, and contains the remains of decayed plant material and a fauna of dwarf invertebrates of marine genera.[99] The most abundant Genesee fauna is that of the "Conodont bed," just beneath the Genundewa member, along Eighteen Mile Creek (17) in western New York.[100] The forms present include the arthrodires *Holonema (Glyptaspis), Coccosteus, Dinichthys, Aspidichthys, Acanthaspis, Stenognathus, Perissognathus, Machaerognathus, Dinomylostoma, Copanognathus, Ptyctodus, Rhynchodus,* and *Palaeomylus;* shark teeth of the genera *Cladodus, Dittodus, Drodus, Acmoniodus* and *Synthetodus;* sharp spines including *Anodontacanthus, Ctenacanthus, Gyracanthus, Machaeracanthus, Stethacanthus, Oestophorus (Sphenophorus),* and *Eczematolepis (Acantholepis);* indeterminate acanthodian fragments; *Onychodus;* of bony fish *Dipterus* teeth (rare) and an indeterminate "ganoid" tooth. The bed is an impure limestone with a maximum thickness of about 4 inches, occurring in lenticular patches and containing large numbers of quartz grains, small pebbles, crinoid stems, fragments of fossil wood, and always more or less broken remains of vertebrates and invertebrate shells. Hussakof and Bryant suggest that the conodont bed represents a sand bar close to a river mouth, with a mingling of marine and fresh-water forms, whereas Chadwick regards it as a marine ablation deposit, in which the fossil fragments have been concentrated *in situ* by the slow washing away of the finer material. Whatever the correct interpretation may be, almost every genus represented is known from black shales or formations still more definitely marine in type.

The Genundewa limestone, or Styliola layer of the Genesee, has elsewhere

98 1908a: 281.
99 Hussakof and Bryant, 1919a: 12, 112, 123, 149.
100 Hussakof and Bryant, 1919a: 12-18.

yielded a few vertebrates. *Dinichthys* is reported from Bristol Center (22), near Canandaigua Lake, and from Genundewa Point (23) on that lake.[101] From several localities along Eighteen Mile Creek (19, 20) are reported *Dinichthys*,[102] *Selenosteus* (?) and *Acanthaspis* (?).[103] This limestone is rich in invertebrates and is unquestionably of marine origin.

From the Genesee shales (?Geneseo or West River) at Canandaigua Lake Hussakof and Bryant[104] cite *Gyracanthus* (or *Machaeracanthus?)*. The shale conditions are essentially marine rather thana fluviatile, but with a sparse fauna and occasional lignites.[105] From the West River shale overlying the Genundewa layer, Hussakof and Bryant[106] report *Holonema* (24) and *Dinomylostoma* (25) in the Buffalo area.

The Sherburne formation, comprising the entire thickness of the Genesee group farther east in New York, has yielded a few vertebrate remains. *Apateacanthus (Pristacanthus)* is described from[107] near Milo, Yates County (26),[108] and *Holonema (Glyptaspis)*[109] from Valois (North Hector) Seneca County (27). At Jefferson, Schoharie County, a scale identified as *Holoptychius* by Eastman is present in a ledge in direct contact with numerous marine invertebrates.[110] At this locality (29) the marine and continental (Onteora in part) facies of the Sherburne formation meet, red-beds predominating from here eastward.

Naples Group (Senecan Series). Clarke[111] reports a single scale of a palaeoniscid from the Middlesex? shales ("West River") at Glenville, Ontario County (31).[112] Numerous scales of this type are present in the same member ("Genesee") at Attica (30a) under conditions comparable to those of the Cleveland shale.[113] *Ptyctodus* is reported with marine invertebrates from the Goniatite or Parrish limestone (Upper Cashaqua) near Naples (34).[114] Eastman cites *Dinomylostoma* as occurring in the marine Cashaqua shale at Mt. Morris (32), Livingston County.[115]

101 Clarke, 1885a: 17; Clarke and Luther, 1904a: 58-59.

102 Eastman, 1897d: Hussakof and Bryant, 1919a: 53.

103 Hussakof and Bryant, 1919a: 18, 81, 101.

104 1919a: 143.

105 Cf. Williams, 1887a: 41; Clarke and Luther, 1904a: 58 etc.

106 Ibid.: 18, 86.

107 "Cashaqua shale" of Eastman, "Naples" of Clarke, but presumably considerably lower in the section.

108 Eastman, 1907b: 81; Clarke 1885: 42.

109 Eastman, 1907b: 147-149.

110 Prosser, Rept. N. Y. State Geol. 1897: 162 (1899); Eastman, 1899f: 321; 1907b: pl. 7.

111 1885a: 20.

112 Later, however, (N. Y. State Mus. Bull. **152**) he states that palaeoniscids are confined to the Rhinestreet.

113 Williams, 1887a: 31-32.

114 Clarke and Luther, 1904a: 62; Eastman, 1907b; 72.

115 Eastman, 1906d: 23; 1907b: 151-156.

Ctenacanthus is described from the true Ithaca, at the base of the Naples Group in central New York, at Six-Mile Creek (33), Tompkins County, New York, by Eastman.[116] The Ithaca beds are essentially marine, and the locality is some 35 miles west of the area of transition of the lower Naples to the continental conditions of the true Oneonta.

Holoptychius has been described by Newberry [117] from the Oneonta at Delhi (37), Delaware County, New York. The environment of the fossil is described as "Catskill sandstone," and the Oneonta at this place is composed of terrestrial red beds.

From the same locality, at Delhi (37), Delaware County, New York, ("Delphi" *in errore),* Eastman [118] cites *Dinichthys* from the "Oneonta." We know no record of the circumstances of the find. Although the true Oneonta is here composed of red beds of presumably terrestrial origin, it is overlain by marine Kattel beds in which *Dinichthys* is normally to be found. *Holonema* and *Dinichthys* are reported from the Oneonta at Oxford (35), Chenango County, New York.[119] Both are in a series of greenish gray sandstones and red shales with numerous land plants and two invertebrates, *Amnigenia* (fresh water) and *Leptodesma.* Brackish deltaic conditions are suggested.

The lower Enfield in central New York (39) has yielded a single tooth of *Dipterus,* associated with plant remains, "a few frail molluscus" (kind not stated) and what appears to be the head plate of a dinichthyd.[120]

The largest faunal assemblage from the Naples group is that from the Attica ("Rhinestreet" or "black Naples" = Enfield, Upper Naples) shale in the Buffalo region (46-48, 49), where Hussakof and Bryant [121] list the following from the Hatch, or higher portion: *Coccosteus, Dinichthys, Stenognathus, Selenosteus, Dinomylostoma, Acanthaspis,* and *Callognathus* [122] (all arthrodires), the ostracoderm *Phyllolepis,* a few "shark" types, including *Dittodus* and *Atopacanthus,* and the palaeoniscid *Rhadinichthys. Cladoselache* is cited from the basal, or true Rhinestreet portion, (40), and from the same horizon at North Evans (41) Eastman lists *Rhadinichthys devonicus.* The Attica comprises a thick mass of dark bituminous shales.[123] Marine invertebrates of pelagic types are present but rare (only seven species), particularly rare in the black bands in which the fish occur. From the true Rhinestreet shales near Sparta (42), Livingston County, Clarke [124] has reported numerous scales and even some partial specimens of *Rhadinichthys (Palaeoniscus),* an acanthodian *(Acanthoëssus?),* and undetermined fish remains. The shales

116 Eastman, 1907b: 77.

117 Newberry, 1889a: 114-115; Eastman, 1907b: 168.

118 Eastman, 1907b: 133, 204.

119 Prosser, 15th Rept. N. Y. State Geol., 1895: 149; Eastman, 1907b: 133, 139.

120 Williams, 1882a.

121 Hussakof and Bryant, 1919a: 18-19.

122 Eastman, 1907b: 17.

123 Houghton, Bull. Buffalo Soc. Nat. Sci. **11**, 1914; Clarke and Luther, 1904a: 32-33; Luther, Bull. N. Y. State Mus. **99**: 25-26, 1906.

124 1885a: 38, 41-42; Clarke and Luther, 1904a: 62.

here are distinctly bituminous in nature; plants of several types were associated; in the same strata, at some distance, but associated with a few indeterminate fish remains, were found a very few invertebrate shells and several conodont species.

Holonema is present in the "Green conglomerate" at the contact of the Oneonta and the basal Kattel, (Upper Ithaca with Lower Enfield) at Greene (38), Chenango County. The beds in which the vertebrate was found are devoid of fossils; there are barren continental Oneonta deposits below, but marine invertebrates are present in the overlying strata.[125]

Vertebrates are reported from the (generally marine) Kattel shale (basal Upper Naples = Rhinestreet) at several localities in eastern New York. From this formation at Franklin (44), Delaware County, Newberry described *Holonema*, on the basis of specimens collected by Orton. This is presumably from a hill which a local collector (Way) showed to Hall and Orton, and in which marine "Chemung" invertebrates are present.[126] *Dipterus* (50?),[127] *Atopacanthus (Apateacanthus)* (36?),[128] and *Onychodus* (44) [129] are also cited from here, but we have no record of the immediate environment of the finds. These normally marine forms are to be expected in the Kattel rather than the barren red Katsberg beds also present above. *Dinichthys*, *Onychodus*, and *Rhynchodus* were discovered in a cut near Franklin Station (43), Delaware County. The beds here are olive shales and sandstones of the Kattel formation, and contain many marine invertebrates.[130]

Holonema is present in company with numerous marine invertebrates in the Upper Enfield formation at Port Crane (51), Chenango County, New York.[131] The region is near the boundary of the deltaic deposits (Katsberg at this horizon) but still definitely on the marine side. *Holoptychius*, *Bothriolepis*, and "Onchus" are described by Eastman [132] from abraided fragments in the "Catskill" (Enfield = Katsberg) of the Ontario and Western R.R. tunnel between Merrickville and North Walton (50), Delaware County, New York. The fish remains occur chiefly in red shales in association with plants and *Lingula*. In interbedded green and bluish shales, with little or no fish remains, are occasional *Leiorhynchus* (marine braciopod) shells.[133]

Chemung Group (Senecan Series).—Bryant [134] has recently described

---

125 Clarke, 13th Rept. N. Y. State Geol. **1893**:545, 1894; Prosser, Rept. N. Y. State Geol. **1895**:151, 1898.

126 Hall, Can. Nat. and Geol. **7**:378, 1862; Newberry, 1889a, pp. 84-85.

127 Eastman, 1907b; pl. 7, p. 162.

128 Hussakof, 1913a: 247-248 ["Onondaga" in error for Oneonta?).

129 Newberry, 1899a: 99-100.

130 Prosser, Rept. N. Y. State Geol. **1897**:111-112, 1899; Eastman, 1899a, 1904e: 297; 1907b: 70, 139, 169, pl. 2, 1908a: 131-132.

131 Prosser, Rept. N. Y. State Geol. **1895**: 161-162, 1897.

132 1899f: 317-327; 1907b: 51, 74.

133 Prosser, op. cit., 113-114.

134 N. Y. State Mus. Bull. **281**: 41-46, 1929.

Coccosteus involutus (angustus preoccupied) from the "Rhinestreet" of Silver Creek (58), New York. This horizon may be Pipe Creek, Dunkirk, or a black band in the Hanover shale (all marine) of the Chemung group; the Rhinestreet is not exposed here. Gross [135] has identified the form as pertaining to the Wildungen genus *Leptosteus*.

Williams has described a plate of *Aspidichthys* from the Upper Portage ("Nunda") of Varysburg (53), Wyoming County, New York.[136] This is the only fossil in a sandstone layer, but marine fossils are present a short distance above and below, with no mention of an erosional unconformity. At High Point (54), Ontario County, New York, Clarke [137] lists *Rhynchodus* and *Cladodus* from the Chemung (High Point = "Nunda"); he gives full geological data, showing unquestionable marine conditions.

Many vertebrates have been collected from Gulf Brook, near LeRoy, Bradford County, Pennsylvania, by A. T. Lilley, and mainly described by Newberry and Cope. Lilley, Leslie, and Kindle have given the (true) Chemung section here from which most of these finds have come. The horizon is mostly that of the Wellsburg, whicmh is transitional between the marine upper Chemung to the west and the continental Montrose to the east, and (stratigraphically) between the marine Cayuta beneath and the red Blossburg above. The lower portion of the beds is essentially marine in nature. In Kindle's zone 24 (Cayuta) (52), *Dinichthys* and *Onychodus* are found in a limestone, in zone 45 ((Wellsburg) (56), *Dipterus* occurs in bluish shales and shaly sandstones; in both cases there is a marine invertebrate fauna. Presumably from the higher of these levels (57?) come also *Ctenacanthus, Gyracanthus, "Ctenodus," Oestophorus (Sphenophorus),* and *Phyllolepis* (the last two associated *fide* Eastman).

The upper part of the Gulf Brook section (57), is marked by the appearance of red beds, the comparative infrequency of invertebrate faunas marking a transition toward "Catskill" conditions. In zones 74-77 Kindle lists *Holonema, Bothriolepis, Holoptychius* and *Coccosteus*. These zones inclunde variegated shales, an iron ore layer, and a thin reddish crinoidal limestone. No invertebrates are reported in these horizons by Kindle except the presence of the crinoidal material. Lilley notes *Bothriolepis* at two levels, associated in red beds with both marine invertebrates and ferns; he reports *Holoptychius* in a fossiliferous brown sandstone next beneath the zone containing the upper *Bothriolepis*. Brackish deltaic conditions are suggested for these upper levels.[138]

---

135 Paläont. Z. **14**:46-48, 1932.

136 Williams, 1887a: 42-43.

137 1885a: 72; Clarke and Luther, 1904a: 64.

138 Claypole, 1883a, 1884a: 489; Lilley, Proc. Amer. Phil. Soc. **21**:304-305, 1884; **23**:291-296, 1886; Newberry, 1899a; 85, 94, 97-98, 101, 112; 1897a: 303; Cope, 1892*l*; Leslie, 2nd Penn. Geol. Surv. Summ. Final Rept. **2**:1448-1450, 1892; Kindle, U.S. Geol. Surv. Bull. **244**:92-106, 1905; Eastman, 1907b; 52, 115, 116, 156; 1917a: 248. Some material from this locality described as *Pterichthys* and *Bothriolepis* appears evidently to pertain to *Holonema*.

At Tioga (55), Tioga County, Pennsylvania, *Palaedaphus (Heliodus)* has been found in marine Wellsburg strata.[139]

Clapole[140] described *Holonema ("Pterichthys")* from the Chemung (Montrose or Cayuta?) of Susquehana County (61), Pennsylvania, but the specimen was not found *in situ*, and the area is one of transitional conditions. *Holoptychius* occurs in the Montrose formation at Skinners Eddy (66), Bradford County, Pennsylvania, in cross-bedded red sandstones and gray shales barren of other fossils.[141] Continental conditions are indicated. Newberry[142] described a good specimen of *Glyptopomus* from a quarry at the mouth of Mehoopany Creek (60), Wyoming County, Pennsylvania, with an implication of typical "Catskill" conditions. The beds here are of terrestrial origin, and belong to the Montrose formation. *Bothriolepis* and *Holoptychius* ar reported by Claypole[143] from Penn Township, Perry County, Pennsylvania. The vertebrates occur in extensive red shale beds containing plant fossils in association with the fish, but no invertebrate remains. In Orange Township, Columbia County, Pennsylvania, White[144] cites *Holoptychius* in a red sandy shale with no other fossils. He reports scales and teeth of *Holoptychius* at Catawissa (59), Columbia County, Pennsylvania. Two invertebrates are found in the beds, *Lingula* and *Pleurotomaria*.[145] The former, at least, is often found in seemingly brackish situations (associated with land plants, for example); deltaic conditions are suggested. This is perhaps the locality whence Leidy[146] obtained crossopterygian teeth *(Apedodus)* from the "old red sandstone." *Holoptychius* is found in a typical "Catskill" alternation of red shales, sandstones and flagstones at Coxton Narrows, Luzerne County, Pennsylvania. The beds contain no fossils but plant remains and fish.[147] *Holoptychius* is also reported at Clinton, from Clinton Township, Factoryville, Wyoming County, Pennsylvania, in a "greenish clay rock." The sediments of the region are in general barren "Catskill" deposits.[148]

Canadaway Group (Chatauquan Series).—Eastman[149] describes *Gamphacanthus (Heteracanthus)* from the "Portage" of western New York. No details are given. The western beds usually termed Portage in the past are in great measure higher than the true Portage, and the specimen very probably pertains to the group under discussion. In general the beds of this horizon and area are definitely of marine origin.

---

139 Sherwood, 2nd Geol. Surv. Penn., Rept. Progress Geol. Bradford and Tioga Counties **G**: 88, 1878.

140 1883a.

141 Sherwood, op. cit.: 21, 1878.

142 1878a; 189-190; 1889a: 117.

143 1883c: 279, 2nd. Geol. Surv. Penn., Rept. Prog. **F**:74, 1885.

144 White, I. C., 1883a: 217.

145 White, op. cit.: 59.

146 1856a: 165.

147 Cope, 1897c: 75.

148 Ibid.: 74-75.

149 1907a: 82.

Holoptychius [150] is found at East Smithfield, Bradford County (62), in soft red Mansfield shale with ferns and fucoid markings, but other fossils. Continental conditions are implied. Sherwood [151] notes fish remains in the "Chemung" (Mansfield) near Mansfield (63, 64), Tioga County, Pennsylvania, in association with marine invertebrates. Hussakof and Bryant [152] report *Holoptychius* from this bed, which is composed of iron ores. We are here in an area transitional between marine Canadaway ("Chemung") strata to the west and the continental Blossburg to the east.

Sherwood [153] describes the "Red Rock" fish bed at Blossburg (68), Tioga County, Pennsylvania, from which came *Sauripterus, Holoptychius* scales, and *Bothriolepis*. The beds are red shales and sandstones (Blossburg) full of fish remains, but otherwise barren.

At South Mountain (70), near LeRoy, Bradford County, Pennsylvania, occurs a thick series of Blossburg beds of continental "Catskill" type, quite devoid of invertebrates. This was discovered by Lilley, and visited in his company by Cope, who reports finding *Bothriolepis, Coccosteus,* and some crossopterygian *(Holoptychius?)*. Kindle reports abundant *Bothriolepis* at one level.[154]

A *"Ctenodus" fleischeri* was sent to Newberry [155] from Troy (69), just to the north of LeRoy, and *Bothriolepis* is also reported from Troy by Hussakof and Bryant [156] without further particulars. The Blossburg beds are present here as at LeRoy, and may have been the source of these specimens.

At Seeley Creek (67), Tioga County, Pennsylvania, in the Blossburg beds along a branch of Lamb's Creek, about four miles northwest of Mansfield, is a famous collecting locality, which has been chiefly worked by Sherwood. Many specimens from this county described by Newberry and Cope are specifically stated to have come from this spot, and other specimens described from Tioga County without further specification by these writers and by Leidy undoubtedly came from this place. The list includes *Dipterus sherwoodi, D. radiatus, Holoptychius, Bothriolepis (Stethacanthus)* and *Holonema* (in part). The fish beds are red shales somewhat mottled with green, containing otherwise only plant remains and a single specimen of *Orthonota*. The continental origin of the strata seems certain. *Gyracanthus* has been found in association with *Holoptychius* at this locality, not however in the Blossburg beds, but in a loose boulder of green sandstone, apparently derived from the overlaying

---

150 Sherwood, op. cit.: 49.

151 2nd Geol. Surv. Penn., Rept. Progress **G**:60, 1878; Kindle, Bull. U. S. G. S. **244**:118-121, 1905.

152 1919a: 176.

153 2nd Geol. Surv. Penn., Rept. Progress 1878g: 48-49; Leslie, ibid., Summ. Final Rept. **2**:1458, 1892.

154 For references see Gulf Brook, LeRoy, under Chemung.

155 1897a: 302-303.

156 1919a: 25.

Rushford strata, or higher, (Upper Canadaway), in beds usually termed "Oswayo" or "Pocono."[157]

A large and heavy *Dinichthys* jaw was collected near the mouth of Canadea Creek (65), in the lower part of the Canadea shale. The specimen was found in place in the shale, and is a marine occurrence.[158]

Dipterus occurs in the Rushford (or perhaps higher) strata at East Rushford (71), Allegany County, New York. The occurrence of the fossils, which are in a pebble conglomerate full of worn fish bones and a few morine invertebrates, is suggestive of a beach or bar deposit.[159]

Conneaut Group (Chatauquan Series). Eastman[160] describes *Ctenacanthus* from the vicinity of Friendship (73), Allegany County, New York, in beds (Cuba?) which contain what apepars to be a typical marine "Chemung" facies. Chadwick has collected a fine spine of *Ctenacanthus* or an allied genus in the Cuba sandstone near Greenwood (74), New York.[161] A scale of *Holoptychius?* was found in a sandstone (Volusia?) in association with many marine invertebrates at Wellsville (75), Allegany County, New York.[162] There are strong indications that the strata grade into "red beds" at a short distance from the site of this discovery.

Dinichthys was found in Greenfield Township (76), Erie County, Pennsylvania in a slab containing a number of marine invertebrates, and about 100 feet above the base of the Chadakoin.[163]

Conewango Group, (Bradfordian Series).—At Little Genesee (83), Allegany County, New York, *Dipterus* has been found in a pebble conglomerate (Wolf Creek?) suggestive of a beach or bar deposit.[164] *Onchus rectus* is found in the marine Le Boeuf sandstone ("3rd Oil sand") in Erie County (79), Pennsylvania.[165]

Eastman[166] mentions *Gyracanthus sherwoodi* at Learn Hill, Ischua (80), Olean (81), and Portville (82), New York. The fossils occur in the Wolf Creek Conglomerate, a formation both marine and terrestrial in affinities.

Butts[167] lists *Bothriolepis, "Ctenodus," Holoptychius,* and *Gyracanthus* from "Zone 7" (between the Salamanca and Wolf Creek formations) of the

---

157 Leidy, 1856s: 163-164; Newberry, 1875a: 61-62; Sherwood, 2nd Geol. Surv. Penn., Rept. Prog. Geol. Tioga Bradford Counties **G**:79-80, 1878; Newberry, 1889a: 19, 85-87, 101-102, 108-112, 118-119, 120, 266; Cope, 1891b: 456-457; 1892l: 221-222, 225; 1897c: 73-74; Leslie, 2nd. Geol. Surv. Penn., Summ. Final Rept. **2**:1459, 1892; Eastman, 1907b: 51, 162; 1917a: 240; Hussakof and Bryant, 1919a: 25, 174, 175-176.

158 G. H. Chadwick, *in litteris.*

159 Williams, 1887a: 61-63, 71-79.

160 1907b: p. 77.

161 G. H. Chadwick, *in litteris.*

162 Williams; 1887a, p. 78.

163 Hussakof and Bryant, 1919a: 54-55.

164 Williams, 1887a: 61-63, 87-89.

165 Hussakof and Bryant, 1919a: 168.

166 1907b: 88, 201; Butts, 1903a: 991.

167 1903a: 990-995.

Conewango series, in Olean Quadrangle (84) Cattaraugas County, New York. This zone consists in the main of red shales lacking invertebrate fossils, but there are thin layers of sandstone or "mud-rock" with marine forms. The conditions are suggestive of a deltaic deposit. At Bradford (87), McKean County, Pennsylvania, scales of *Holoptychius* and *Sauripterus* occur in a thin layer of fine-grained light green argillaceous shale in the middle (Salamanca?) part of the Conewango. No other fossils are present. There are marine beds above, but the strata beneath, with similar green layers, appear to be terrestrial.[168]

Along the Alleghany River at Warren (85), Pennsylvania, are extensive exposures of the Upper Devonian and Carboniferous. Here many vertebrate specimens have been collected by Randall, Beecher, and others, and described mainly by Newberry and Eastman. Certain spines are said to have come from the Carboniferous of this section, but the greater part of the material probably is derived from a fish bed in the Conewango ("Chemung") described by Randall. This is a local pebble conglomerate, containing teeth and bones generally abraided and eroded. No invertebrates are mentioned, but Chemung marine invertebrates appear to be presnt both above and below in the section exposed. The conditions suggest a river mouth bar deposit and a quite possibly mixed faunal assemblage. Forms lister from here (although some may not be from this particular bed) include *Dinichthys, Cladodus,* the dipnoans *Dipterus, "Ctenodus"?, Palaedaphus (Heliodus)* and *Ganorhynchus, Holoptychius (Apedodus),* and *Rhadinichthys,* as well as spines which are presumably from higher, Mississippian exposures.[169]

The New York-Northern Pennsylvania series considered above gives both marine and continental types of deposits representing practically the entire extent of the upper Devonian. Below are listed other North American beds of late Devonian age. No attempt has been made to arrange them in stratigraphic sequence. First are listed deposits of seemingly continental types, followed by those of marine origin. The fresh-water finds are either from the eastern fringe of the continent, or far west. The marine deposits are almost entirely in the middle west.

Scaumenac Bay, Quebec.—This locality is the most representative of the upper Devonian fresh-water deposits. Genera present include *Acanthoessus (Acanthodes), Diplacanthus, Euphanerops, Cephalaspis, Coccosteus, Holoptychius (Glyptolepis), Cheirolepis, Scaumenacia, Eusthenopteron,* and *Bothriolepis,* the last three constituting perhaps 95% of the specimens discovered. The evidence for the freshwater character of this deposit (mainly shales with occasional sandstones) is, although chiefly negative, fairly conclusive. Plant remains are present and despite the abundance of fishes and the numerous collections made from this locality, not a single specimen of any invertebrate

168 Williams, 1887a: 101.

169 Randall, 2nd Geol. Surv. Penn. Rept. Progress **I**: 1874, 50-55, (1875), and ibid., 14, 306, 1883; Newberry, 1889a: 85, 89-91, 95-100, 102-103; Leslie, Summ. Final Rept. 2nd Geol. Surv. Penn., **2**:1492-1496; Butts, New York State Mus. Bull. **69**: plate 2, 1903; Eastman 1907b; 63, 75, 77, 87, 137-138, 166, 172, 212, pls. 1, 4; Hussakof, 1908: 58; Eastman, 1917a: 249-250, Hussakof and Bryant, 1919a: 171.

has ever been reported.[170] Ells and Low suggested a lake deposit, and Kindle, the most recent worker, says it is "a continental deposit laid down in lagoons, fresh water lakes, or along wide river valleys."

Upper Devonian, East Greenland. Extensive Upper Devonian deposits in the general neighborhood of Franz Joseph Fiord have been explored by various Scandinavian expeditions, and fish remains, including the ostracoderm *Phyllolepis*, the antiarchs *Bothriolepis, Remigolepis,* and *Asterolepis,* the arthrodire *Groenlandaspis* and crossopterygians including *Holoptychius* and perhaps other genera, have been discovered. It is of interest that in these beds have also been foun dthe only known Devonian amphibians. The beds are of typical "Old Red-Catskill" type—gray to red sandstones and shales barren of invertebrate remains.[171]

Upper Devonian of Ellesmere Land.—Kiaer [172] describes a number of fish remains from "series E" of Ellesemere Land, an Upper Devonian series of "Old Red" facies. Fish are found at various horizons. There are in most cases no other fossils except ferns. In one instance however, many fragmentary fish remains were found in a conglomerate containing both numerous plant remains and numerous mussels identified with doubt as *Plitonia* cf. *cylindrica* Hall. This locality is suggested to be a brackish lake in an otherwise continental set of beds. The fish remains include the ostracoderm *Psammosteus,* a large arthrodire compared with *Aspidicthys,* the antiarch *Bothriolepis,* and crossopterygians including *Holoptychius, Glptaspis,* and *Osteolepis.*

Elbert Formation, Colorado.—Bothriolepis, Holoptychius and *Coccosteus* (?) are described from the Elbert Formation,[173] a succession of varicolored calcareous shales, thin limestones and occasional quartzite beds less than 100 feet thick resting unconformably on the Cambrian Ignacio Quartzite in southwestern Colorado. No invertebrates are present; salt crystals are reported; there is no basal conglomerate. The facts suggest a lake, generally fresh but suubject to dessication. *Dipterus* and *Synthetodus* were later described from the Elbert in Florida Valley in the Ignacio Quadrangle. We have no details of this find, but conditions in this region seem to be generally comparable to those in the Needle Mountain region described by Cross.[174] *Holoptychius* (?), lungfish scales and arthrodire plates are described by Cross [175] from the Parting Quartzite at Aspen, Colorado. This formation is heterogenous in color and composition (shale, dolomite and quartzite); it is similar stratigraph-

170 Whiteaves, 1887a; Kindle, Can. Geol. Surv. Summ. Rept. **1928**:83-89, 1929, etc.

171 Smith, Woodward, 1900H; Heintz, Skrifter om Svalbard og Ishavet, Oslo, Nos. **30**, 1930, and **42**, 1932; Stensio, Medelelser om Grønland, **86**(1) Copenhagen, 1931.

172 1915a: 17-56.

173 Cross, 1905c, p. 4; Amer. J. Sci. **18**(4):248-250, 1904; Eastman, 1904b; also Needle Mountain Folio (131) U.S.G.S., p. 4, 1903.

174 Howe, U. S. Geol. Surv. Prof. Paper **21**:8; Eastman 1915a.

175 Amer. J. Sci. **18**(4):251-252; Kindle, Ibid. **22**(5):222-239, 1931; Behre and Johnson, Ibid. **25**(5): 471-486, 1933.

ically and lithologically to the Elbert Formation of the same state. *Grand Canyon, Arizona. Bothriolepis* and *Holoptychius* have been found in the Grand Canyon region in hollows suggestive of ancient stream valleys eroded into the surface of the Tonto Limestone. The fillings have been variously described as purple sandstones, calcareous sandstones, or an impure dolomite. The material exhibits cross-bedding; there are no traces of invertebrates except worm borings.[176] The deposit seems reasonably of fresh-water origin.

Devonian of Wisconsin.—Numerous fish have been reported from a Devonian formation in Wisconsin formerly correlated with the Hamilton, but now regarded as somewhat later in age. The forms found include the typical arthrodire *Dinichthys*, the ptyctodonts *Ptyctodus, Rhynchodus*, and *Palaeomylus*, the fish spines *Machaeracanthus Eczematolepis (Phlyctaenacanthus) Acantholepis, Gamphacanthus (Heteracanthus)* and *Oestophorus (Sphenophorus)* as well as *Onychodus, Cladodus* and the arthrodire *Holonema (Glyptaspis)*. Almost all of these remains are from the quarry of the Milwaukee Cement Company in Milwaukee. The beds here are an impure dolomite, containing a considerable number of marine invertebrates.[177]

Wapsipincon Formation, Iowa.—*Ptyctodus* and perhaps *Dinichthys* are present in this marine formation in Iowa.[178]

Cedar Valey Limestone, Iowa-Illinois.—This limestone is in lithology, wide extent and abundance of marine invertebrates typically marine. Fish remains have been found in it in a number of localities.[179] The most abundant finds are from the quarries north of Waverly, Iowa. The remains included *Onychodus*, scales referred to *Holoptychius* (?), a tooth assigned to *Ganorhynchus* (perhaps *Synthetodus?)*, the fish spine *Gamphacanthus (Heteracanthus)* and the ptyctodonts *Ptyctodus* and *Rhynchodus*. Little is known of the exact horizon of the remains, but they are believed to be from three beds, all yellow limestones, one unfossiliferous, the other two with a few fossils, mainly *Spirifer.*[180] *Onychodus* has been found in the lowest member of the Cedar Valley in East Waterloo Township, Blackhawk County, Iowa, in a limestone containing a few invertebrate marien fossils (crinoid stems, *Atrypa).*[181] *Phoebodus, Rhynchodus, Ptyctodus* and *Gamphacanthus (Heteracanthus)* are also reported by Eastman from Waterloo. The last and the armor of a "placoid" *(Dinichthys)*[182] have been found near Rock Island, Illinois, with an abundant brachiopod fauna. A *Dipterus* tooth was found at Fairport, Muscatine

---

176 Walcott, Amer. J. Sci. **20**(3):224-225, 1880; Schuchert, 1918a; Noble, U. S. Geol. Surv. Prof. Paper **131**:50-52, 1922.

177 Eastman, 1899b, 1907b: 15-16, 1908a: 276-279; Cleland, 1911a; Hussakof and Bryant, 1919a: 50-51, 104-105, 108, 116-117, 119, 164.

178 Norton, Iowa Geol. Surv. **9**:440,1899; Eastman, 1908a: 48.

179 Eastman, 1908a: 106-107, 124-127, 134-140, 196, 213, etc.

180 Norton, Iowa Geol. Surv. **16**:352-353, etc., 1905.

181 Arey, ibid.: 425-426, 1905.

182 Udden, 1897a; Lindahl, 1897a; Eastman, 1902d.

County, Iowa, associated with a rich marine invertebrate fauna, and another tooth of the same genus at New Buffalo, Iowa.[183]

Manitoban Limestone.—*Ptyctodus, Rhynchodus, Dinichthys, Aspidichthys* and *Onychodus* have been collected in Devonian rocks in the vicinity of Lakes Manitoba and Winnipegosis, Manitoba. The zone yielding these forms consists of calcareous gray shales containing seven species of marine invertebrates; the zones above and below are highly fossiliferous.[184]

Jennings Formation, West Virginia.—Armor plates of the arthrodire *Holonema (Glyptaspis)* are reported from the Parkhead member of this formation southwest of Hancock, West Virginia. The exact horizon is not described. The Parkhead consists of shales interbedded with massive sandstones, with an abundant marine invertebrate fauna; is is the equivalent of the Enfield formation of New York.[185]

Huron Shale, Ohio Region.—*Xenodus (Goniodus), Dinichthys, Callognathus, Stenosteus, Aspidichthys, Onychodus* and *Rhadinichthys* are the only vertebrates reported from the carbonaceous Huron shale (Senecan) of Ohio and Ontario.[186] Invertebrates, except an occasional *Lingula* and conodonts, are exceedingly rare, and plant materials, ranging from spore cores to logs, are common. We find it difficult to believe in the typically marine nature of this formation at such a place as that cited by Stauffer [187] at Kettle Point, Ontario, where *Rhadinichthys* is abundant with numerous plant remains.

New Albany Formation, Kentucky.—This black shale is essentially similar lithologically and in faunal content to the last, except that marine invertebrates are less rare.[188] The vertebrates are similar to those of the Huron and the Senecan black shales; Eastman [189] lists *Dinitchthys, Holonema (Glyptaspis), Aspidichthys, Ptyctodus* and *Rhynchodus,* while Hussakof has described *Dinomylostoma* [190] from these beds, and a *Stethacanthus* also described by him from Junction City, Kentucky, is presumably from the New Albany (the Waverly appears not to be present in this area).

State Quarry, Hackberry, and Sweetland Creek Beds, Iowa.—Vertebrates have been found at several Upper Devonian localities in Iowa. In Johnson County, *Ptyctodus, Synthetodus, Dipterus, Conchodus,* and *Dinichthys* are found in the State Quarry Limestone; the first three are abundant, particularly *Ptyctodus.* The fish are found in an 18-inch layer near the middle of the formation; this layer is not otherwise noticeably different from the remainder of the limestone. The considerable marine invertebrate fauna and the lithology

183 Udden, 1899a; Eastman, 1907b: pl. 4.

184 Tyrrell, 1892a: 162, 163, 168, 183, 192, 194, 209; Whiteaves, 1892a: 353-356; Kindle, Rept. Geol. Surv. Canada. **1912**:248, 1914.

185 Swartz, 1913a: 415-417, 700-701.

186 Newberry, 1874g: 152ff.; 1889a: 57-59, 64-65, 69-74; Eastman, 1907b: 18-19; Branson, 1908b: 94; Prosser, 1913a; Kindle, 1914c; 286.

187 1915a; 182-184, etc.

188 Foerste, Bull. Kentucky Geol. Surv. No. **7**:102-114, 1906.

189 1907a: 133, 147-149, 172, pl. 13; 1908a: 155, 279, 281-282.

190 1913a.

suggest a comparison with the modern coquina limestones of Florida.[191] Dr. C. L. Fenton informs us that *Ptyctodus* and lungfish teeth have been collected from the Marine Hackberry, of approximately the same age. *Ptyctodus* (abundant) and *Synthetodus* and *Rhynchodus* (one instance each) are noted by Udden[192] at five localities in the Sweetland Creek beds of Muscatine County. Udden considers the deposit to be of marine nature.

Upper Devonian, Louisiana, Missouri.—Branson[193] has collected *Dinichthys, Mylostoma, Ptyctodus, Helodus* and *Eoörodus* from a one-foot layer of dark blue shale underlying the Louisiana Limestone. Marine invertebrates are found in limestones above and below this layer and in sandy stringers through the shale itself.

Ouray Formation, Colorado.—A tooth of *Cladodus* was found by Cross[194] in the lower (Devonian) portion of the Ouray Limestone, which contains a typical marine invertebrate fauna.

Upper Devonian of Alberta.—Helodus has been collected from Roche Miette and Bullrush Mountain, Alberta, from limestones which at the former locality contain a marine invertebrate fauna of Devonian aspect.[195]

Upper Devonian of Wyoming.—Branson[196] describes *Dinichthys, Acanthaspis* and *Ptyctodus* from a sandstone near Lander, Wyoming. No details concerning this presumably marine localitiy are given.

Cleveland Shale.—The richest and most spectacular of American early fish faunas is that of the Cleveland Shale. The age of this deposit has been much debated. There is considerable evidence for its assignment to the Mississippian rather than the Devonian, but since its time of deposition represents the climax of Devonian marine fishes, we may well include it here. We need not in most instances mentain specific finds or localities, since conditions appear to have been in general rather uniform. The fauna has been listed recently by Cushing;[197] almost all the types are either cladoselachian sharks—*Cladodus, Monocladodus, Cladoselache, Ctenacanthus, Phoebodus*—or arthrodires—*Coccosteus, Dinichthys, Titanichthys (Brontichthys), Hussakofia, Mylostoma, Selenosteus, Callognathus, Diplognathus, Dinognathus, Trachosteus, Stenognathus.* Other forms include only the fin spine *Hoplonchus*, the actinopterygian "ganoids" *Rhadinichthys* and *Tegolepis (Actinophorus)* and the lungfish *"Ctenodus"*; these latter forms are for the most part rare. *Tegolepis* and *"Ctenodus"* are known only from single specimens. *Rhadinichthys*, however, is represented by scales, often numerous, in several collections. We need not repeat in detail the arguments as to the nature of the Cleveland

191 Calvin, 1896a: 72-88; Eastman, 1898a: 108 ff; 1908a: 135-139, 215, 220-235, etc.

192 J. Geol. **7**:65-75, 1899.

193 1922a.

194 Cross, Needle Mt. Folio, U. S. Geol. Surv. Folio **131**:4, 1905; Kindle, Bull. U. S. Geol. Surv. **391**, 1909.

195 Lambe, 1913d: 17-20.

196 Bull. Geol. Soc. America **40**:245, 1929.

197 U. S. Geol. Surv. Bull. **818**:38, 1931.

shale. The circumstances are similar to those found in the case of the other black shale formations of the upper Devonian: invertebrates are rare and consist almost entirely of a few species of brachiopods, particularly *Lingula;* plant fragments are not uncommon.

Upper Devonian—Summary.—The very numerous Upper Devonian fish localities appear to exhibit every variation from marine to fluviatile or lacustrine conditions. The great majority of the finds are from black shale deposits. They give us a picture of an essentially marine vertebrate fauna composed for the most part of numerous arthrodires and cladodont sharks. In sharp contrast is the seemingly fresh-water fauna exhibited in a number of deposits of "Old Red" or "Catskill" type, in which antiarchs and crossopterygians such as *Bothriolepis* and *Holoptychius* are the most abundant and widespread forms. Both salt and fresh-water vertebrate faunas were well established in late Devonian, as in later times.

European Upper Devonian—Comparison.—The European Upper Devonian presents a picture comparable to that of America. The marine beds of the Rhineland exhibit a fauna which, particularly in the abundance and variety of arthrodires and the presence of cladodont sharks *(Cladodus, Ctenacanthus),* is comparable with that of the salt-water beds of North America. *Dinichthys* and other large types of arthrodires are, however, almost unreported from Europe, and these beds also contain a possible antiarch of highly specialized type and the first of the coelacanths, an aberrant crossopterygian group known in the marine Mesozoic beds. The Upper "Old Red" reveals a fauna highly comparable to that of the "Catskill" and Scaumenac Bay, with *Bothriolepis* the most numerous form, crossopterygians abundant and other groups comparatively rare.

VIII. Discussion

Classification of data.—In the preceding sections the data concerning early American fish finds have been presented. How shall this varied assemblage of material be assembled in order to facilitate a discussion of its bearing on the question of early vertebrate environment? A clear-cut distinction between definitely marine and definitely fresh-water occurrences is impossible. Obviously in a great proportion of the localities listed we are dealing with deposits which lay close to the shore-line on one side or the other. There are few of the presumed fresh-water localities here cited which all would agree to be beyond any possible "contamination" by dwellers in brackish or salt-water, while in even the most typically marine deposits an occasional stray cadaver floating out from land is far from impossible.

In order to group the material, we have attempted to range the various finds into four classes, numbering them from 1 to 4 in order of their seeming gradation from fresh to salt-water conditions of deposition: 1. Localities or finds for which the evidence is strongly suggestive of fresh-water conditions. 2. Localities in which the evidence is suggestive of deltaic or estuarine and somewhat brackish conditions; where, for example, a few brackish or salt-water invertebrates are present and hence, although the faunal content is presumably

mainly derived from the rivers carrying the sediments, a small admixture of marine fishes is not improbable. 3. Localities or formations which seem certainly to have been laid down in marine waters but in which the situation is such as to suggest near-shore conditions. In such deposits we would expect the main body of the fauna to be of a marine nature; but a certain percentage of fresh-water forms, of types tolerant of considerable variation in saline content of water, and groups in evolutionary transit from one type of environment to another might be expected. 4. The more purely marine formations, in which the presence of a fresh-water cadaver is rarely to be expected.

This classification has been used in drawing up the accompanying tables and diagrams upon which our further discussion is based. Almost all of the finds cited seem to fall reasonably into one or another of these four categories.

The Devonian marine trend.—In Table I the numerous genera composing the various groups are listed, each occurrence of a genus in a formation of the Silurian or one of the major Devonian divisions being represented by a figure showing which of the four above-named classifications appears to be represented. These citations are collected in Table 2.

It is obvious that the number of citations, which in a very rough way suggests the relative frequence of occurrences, shows a steady increase in vertebrate life throughout the periods covered (although the European finds, we believe, would indicate a somewhat higher proportion for the late Silurian and early Devonian). This suggests that, in the vertebrates, we are dealing with a new and rapidly expanding group. This is presumably true to some extent; but it must be pointed out that the Silurian vertebrates, as shown particularly by Stensiö's researches, are not primitive forms but highly specialized and complex types.

Another possibility becomes obvious if the environmental conditions under which this expansion took place be considered (cf. Fig. 1 as well). There is, from the Silurian to the end of the Devonian, an increase in the numbers of forms which are presumably fresh-water dwellers, listed in columns 1 and 2 of Table 2a (It must be remembered that the data are unsatisfactory in one respect—the paucity of representatives in this country of the middle Devonian continental phase). But it is in the sea that the most startling expansion has taken place. There are no definitely marine records of vertebrates in the American Silurian, very few in the lower Devonian; but by the end of that period marine citations outnumber those from presumed fresh-water deposits in a ratio of 7:3. How is this great marine expansion in numbers compared with a relatively stable fresh-water distribution to be explained? The answer would appear to lie in a migration of fishes from fresh water into the seas. If we assume the seas to have been the original home of the group, it is difficult to account for the rarity of marine vertebrates prior to the middle Devonian. This cannot be explained by any assumption that sediments suitable for the preservation of marine vertebrates are absent or rare in Silurian and early lower Devonian horizons, for this is not the fact. There are numerous marine strata dating from these times which appear to be as good potential recipients of vertebrate remains as those of the later Devonian or Missis-

sippian, but vertebrates are not found in them; and we see no way of avoiding the conclusion that there were few or no vertebrates in those seas to be preserved.[198]

While other factors undoubtedly were concerned in this Devonian marine migration, it seems highly probable that the great marine transgression of the middle Devonian, which must have greatly reduced the area in which fresh-water fishes could live, was a considerable influence in forcing seaward migration.

Pre-Devonian vertebrates.—Let us turn from a consideration of this seeming definite Devonian shift from dominantly continental to dominantly marine existence to consider the earliest, pre-Devonian finds. There is no definite evidence of any vertebrate in the Cambrian, and except for the Harding sandstone scraps and a few tooth-like structures from Russia there are no Ordovician remains. Even in the Silurian vertebrate remains are quite rare until near the end of the period (Downtonian), and in the Downtonian, as in the American Silurian, the finds are almost never from marine deposits, but on the contrary are mainly found under conditions suggestive of fresh-water existence.

This situation, contrasting strongly with the dominantly marine surroundings of the upper Devonian finds, is very difficult of explanation under the hypothesis that the sea was the early vertebrate center. Where are the ancestral vertebrates in the older Paleozoic marine rocks? The answer could at one time have been made with confidence that the older vertebrates were soft-bodied and hence not preserved, and that bone or other hard parts became present only in specialized or advanced types; that the vertebrates were really present in the old seas but were practically incapable of fossilization. This is not the place for a detailed discussion of the topic,[199] but the work of Stensiö, Watson, Heinz, and others has during the past decade rendered such a position untenable. It is now generally accepted that in almost every instance early vertebrate types were armored, and that the absence of armor in later types is due to reduction. Only in the case of the sharks is the case unproven, and even here evidence for an early armored condition is accumulating.[200] Although we may theoretically assume an early unarmored stage in vertebrate history, this stage must have been passed through at a very early date, for well developed armor is present in the Harding sandstone vertebrates.

One of us [201] has suggested that the development of armor was associated with the need of protection from eurypterids on the part of fresh-water

198 Gross, who believes in a marine origin for vertebrates, attempts to meet this difficulty by suggesting that "Old Red" conditions were peculiarly suitable for the preservation of fossils (Paläont. Z. **15**: 134, 1933); but why by late Devonian times marine localities should have become much more suitable than the "Old Red" is not explained.

199 See, for example, Gross, op. cit., 1933.

200 As noted later, Broili has just announced the discovery of the shark-like body of a macropetalichthyid, an armored type usually referred to the arthrodires, thus strengthening greatly the argument for shark degeneration.

201 Romer, Science, n. s. **18**:114-117, 1933.

dwellers, so that a hypothesis might be constructed on these lines: that the central vertebrate stock consisted of soft-bodied sea-dwellers, branches of which migrated into fresh waters and there (as exemplified in the Harding sandstone and Silurian material) gained armor in this connection. But this is no real solution to the problem. We have just noted that most Devonian and later vertebrates are probably descended from armored types. Hence hypothetical soft bodied marine forms can have had no direct descendants, and this line of argument also leads to the conclusion that fresh waters were the place of origin of later vertebrates.

If, as the morphological evidence leads us to believe, the ancestral vertebrates did have hard parts capable of fossilization, their absence from marine deposits in the lower Paleozoic seems obviously due to the fact that they did not exist in the early Paleozoic seas. There are very numerous Cambrian, Ordovician and Silurian American marine formations rich in many types of invertebrate fossils, but not one shows us the faintest trace of any vertebrate in normal marine conditions. Further, we are unable to imagine any reasonable hypothesis to account for the lack of preservation of vertebrates in these deposits if they were actually present in these early seas.

On the other hand the known evidence is quite adequately explained by the hypothesis that the lower Paleozoic fishes were dwellers in fresh waters. They are found in the Silurian in deposits of a seemingly continental type which in many cases constitute essentially a first stage in the "Old Red" sequence, and the Harding sandstone remains have been interpreted as pertaining to fluviatile forms.

The rarity of lower Paleozoic fishes may be partially due to the fact that the early vertebrates were restricted in numbers and variety. This restriction in itself may be in great measure attributed to existence only in fresh waters, with a consequent limitation of opportunities for evolutionary radiation. The rarity of specimens seems, however, largely due to the other factors related to this fresh-water life of early vertebrates: (1) water-living vertebrates are in general rare in continental deposits [202]; and (2) continental deposits are in themselves comparatively rare in the Ordovician and most of the Silurian.

The conditions under which vertebrates are found in the European Silurian give a clear demonstration of the adequacy with which the hypothesis of an inland existence for the group fits the known facts. An inspection of the vertebrate record of that period shows that (1) stratigraphically, finds of vertebrates increase rapidly in numbers as the end of the period is approached, and (2) geographically, these finds are increasingly numerous as we pass from south to north. With these findings we may match two elementary facts, common to every textbook, that (1) the late Silurian deposits of Europe become increasingly continental in nature; (2) northern Europe at this time was a continental area, with seas to the south.

---

202 Very little record of fish life is, for example, preserved in such continental beds as the Morrison, the late Cretaceous Dinosaur beds of the Rocky Mountain region, and the White River beds—deposits in which there are abundant remains of land vertebrates.

Food.—Drs. Ruedemann and Raymond, *in litteris,* have raised the pertinent question of food supply as a theoretical argument against the presence of pre-Devonian fishes (and eurypterids) in fresh waters. They point out that the Silurian deposits which we consider as presumably fresh-water in nature have few animal organisms which would be a possible source of food supply, and that since land plants are almost unknown until the Devonian, the plant life upon which animal communities depend as the basic source of their food supply was not present.

This problem is worthy of serious consideration. We do not, however, regard it as an insurmountable difficulty.

Absence of invertebrate fossil material in the derived deposits does not necessarily debar an ancient body of fresh-water as a possible habitat for fishes. Shelled megascopic invertebrates which are potentially preservable under ordinary conditions are far from numerous in modern fresh waters, and play but a small part in the food supply of living fishes. In numerous post-Devonian fish-bearing deposits which are generally conceded to be of fresh-water origin, invertebrate fossils are almost always rare and frequently appear to be entirely absent. If absence of plentiful invertebrates debars a presumed fresh water locality from a position as a possible home of fish life in pre-Devonian times, we should logically carry the same assumption to later periods and thus reach the untenable theoretical conclusion that few if any fish have been fresh water dwellers in any pre-Recent period. Further, we may note that almost all of the pre-Devonian fishes (and many of the early Devonian ones) were jawless ostracoderms, obviously bottom dwelling mud-grubbers incapable of ingesting invertebrate forms of any size. Most of the tiny types of crustaceans which form a large part of the food supply of modern freshwater fishes are almost unknown as fossils (except the ostracods) and we have no knowledge as to when their invasion of fresh waters occurred, although it presumably would have followed closely upon the developments of algal life inland waters. But even these small creatures would probably have been too large for small suctorial ostracoderms.[203]

The almost complete absence of remains of land plants in pre-Devonian deposits does not to us necessarily imply an absence of plant life in pre-Devonian streams. As far as we are aware fresh-water fishes do not in a great measure depend upon trees and other land plants for food, except as their debris is, in the water, transformed into other food materials. The real question is as to the presence or absence of aquatic plant life in pre-Devonian lakes and streams. Of botanic material of this nature we have comparatively little fossil evidence at any period, pre- or post-Devonic. Well developed forests were already present in the middle Devonian (Gilboa) and we find it difficult to believe that the ancestors of these forms had left the oceans for

---

203 Can the origin of jaws have occurred in relation to the development of crustacean life in inland waters?

fresh waters and the land only half a period before. The paleobotanist Seward [204] says that:

> It is difficult to believe that the Devonian floras were entirely derived from highly organized marine algae which had solved the complex problems presented to them as the sea floor was upraised during the Caledonian revolution. The probability is that before the end of the Silurian, and perhaps at a much earlier date, the continents were sparsely clothed with the relatively simple pioneers of a land flora.

The theoretical argument that fresh-water fishes cannot have existed in pre-Devionan times because we do not find their food supply seems adequately answered by the theoretical paleobotanical argument that the basic food materials must have existed.

History of the various early fish groups.—Although the consideration of early vertebrate history as a whole indicates a freshwater origin but a strong trend toward the sea in Devonian times, we would expect to find, and do find, considerable variation in this regard among the various groups concerned. In Table 1 the types of environment under which the numerous pre-Carboniferous genera are found are listed on the 1-4 scheme of classification of deposits described above. The grouping is in some cases not strictly by proper taxonomic units, but is for convenience in handling the material.

Agnatha.—Jawless vertebrates, Agnatha, are, in the form of "ostracoderms" the dominant forms in the Silurian, still common in the early Devonian, rare in later deposits of that period, unknown as fossils later. Presumably the Harding sandstone scraps pertain to one or more ostracoderm groups, but the material is none too good. The Silurian ostracoderms are members of a primitive vertebrate class, but nevertheless are highly complex forms, as shown by recent work, particularly that of Sensiö, and are already divisible into three distinct groups. We are witnessing, in the Silurian and early Devonian ostracoderms, not the beginning of vertebrate history but the end of a cycle most of which is as yet unknown.

Of these ancient vertebrates, the Heterostraci, characterized by presumably paired nostrils and by the usual presence of a well-developed armor in which bone cells are absent, are the commonest forms in the American record, and among the heterostracans the vast majority are of the oval-"shelled" *Pteraspis* type. These last-mentioned forms (including *Cyathaspis, Palaeaspis, Pteraspis, Protaspis, Cryptaspis, Glossoidaspis, Cardipeltis* and *Cyrtaspis)* account by themselves for a majority of all ostracoderm finds, a majority of all known Silurian vertebrates reported from this country, and a considerable proportion of the lower Devonian finds—they are unknown later. The Silurian pteraspids are present in seemingly fresh-water, or, at the most, brackish sediments; the lower Devonian forms in both continental and marine deposits, suggesting thus a drift toward the sea. The seeming abundance of these forms in Silurian and early Devonian formations is, we suggest, perhaps not so much because they were in life overwhelmingly abundant compared with other ostracoderms, but because their trend toward marine existence and a possibility that their envi-

204 Plant Life through the Ages, p. 100, (Cambridge), 1931.

ronment may have been more particularly in the lower reaches of streams may both have tended to a readier preservation of these forms.[205]

The term *Thelodus* is applied in North America to scale-like structures which may pertain to the European genus, a proper heterostracan, but which, in the absence of association with the body form of coelolepids, may well have pertained in some instances to members of other fish groups. *Psammodus* and *Phyllolepis* are late Devonian survivors of the order.

The Heterostraci are believed by Stensiö to be related to the hag-fishes, but there appear to be few positive indications of such an association.

Cephalaspis and related types, the *Osteostraci,* with a bony "horned" head-shield and median nostril, are unknown in North America in the Silurian although found in Europe at that date. There are several Devonian citations from this continent. All these reports are from fresh-water deposits; the European record appears to be essentially similar in nature.

The small anaspids, well-known from Europe through the pioneer work of Traquair, and the more recent researches of Kiaer, are represented in North America only by the single *Ctenopleuron* specimen from the Silurian and a questionable form, *Euphanerops,* from the upper Devonian. Both these are from presumed fresh water formations. In Europe anaspids are also comparatively rare, being found only in the fresh-water Downtonian of southern Scotland and Norway. We suggest that this rarity may be due to the fact that these slim bodied little fishes, obviously the most active of the ostracoderms, were dwellers in inland streams and only rarely would tend to be present in lowland deposits where their preservation might occur.

The problem of the earlier history of the ostracoderms is practically that of the earlier history of the vertebrates as a whole, since almost all pre-Devonian finds are those of ostracoderms. We have no reason to assume an unarmored ancestry except at a remote antecedent stage, since armor of ostracoderm type is present in the middle Ordovician; and we have no reason to assum a hypothetical, inexplicably unrecorded marine history for these predominatingly fresh-water types.

Antiarchs.—The curious small armored placoderms of the order Antiarchi, of which *Bothriolepis* is the best-known representative, are, in North American material, almost entirely confined to the upper Devonian. *Bothriolepis* is reported from a large number of "Catskill" localities, is the most numerous of the many forms at Scaumenac Bay, and is present in Colorado, Arizona, and Greenland; in the last locality *Asterolepis* and *Remigolepis* are also recorded.[206] All these citations are apparently from seemingly fresh-water deposits, with never any associated marine fauna. As far as the American evidence goes the antiarchs are a purely freshwater group. In Europe the overwhelming majority of the finds (Middle and Upper Devonian) are from

205 Dr. Raymond points out that their stout "shells" may have made for better preservation (and also readier discovery by the collector).

206 As noted elsewhere, "Asterolepis" from the Chapman sandstone is probably an arthrodire.

beds of the "Old Red" type. In Europe, however, some marine antiarch material is present in both the Middle and Upper Devonian; however, only in the case of *Ceraspis*, an exceedingly specialized form with a tall "hump" on its back, is this material at all abundant. The evidence as a whole is suggestive of a fresh-water center of distribution, with a highly specialized marine side branch. The origin of the group is unknown, but presumably the antiarchs are closely related to the primitive arthrodires of the Lower Devonian, which likewise appear to have been mainly fresh-water types.

Arthrodires.—This great group of placoderms includes a large proportion of the described fish types of the Devonian (about one third of all genera described from North America, for example). Arthrodires are unknown as yet in the Silurian, but are present in the Devonian from beginning to end (contrary to the usual textbook statement, at least one group, the ptyctodonts, presisted into the early Mississippian). The great majority of the group were marine forms, and in middle and later Devonian times their evolution took place almost exclusively in salt waters. In the "Old Red" type of deposits *Coccosteus* is almost the only arthrodire reported from the Upper Devonian, while in the contemporary marine rocks there are about two dozen arthrodire genera. Besides the giant forms such as *Dinichthys* these deposits contain a considerable number of forms, large to small, of "advanced" arthrodires which may trace their descent from *Coccosteus*, which is found in marine as well as fresh-water deposits in both Middle and Upper Devonian times.[207] *Holonema* is an incompletely known aberrant form very abundant in "Chemung" and "Oneonta" deposits and rare elsewhere; we suggest that this is indicative of a littoral habitat. Widely divergent are the ptyctodonts, purely marine in distribution, and represented almost entirely by jaw plates of a crushing type, *Ptyctodus* being the common genus. These forms are common in both the Middle and Upper Devonian. The systematic position of the ptyctodonts is still in doubt, for although Dollo's assignment of them to the arthrodires is generally accepted, the relationship may be a distant one.

The probable ancestry of the higher or more specialized arthrodires is now believed to lie amongst the acanthaspids, a group known until recently mainly from *Acanthaspis* and *Phlyctaenaspis*, but recently restudied by Heintz[208] on the basis of Spitzbergen material. This group is represented in America in Middle and Upper Devonian deposits by *Acanthaspis*, found in half a dozen marine formations but never in fresh-water deposits. This would in itself suggest that arthrodire history throughout has been in marine waters. But the American Lower Devonian record shows a different story. Primitive arthrodires are present in two places in marine rocks—in the Chapman sandstone and the "Madison" of Blacksmith's Fork, Utah—for a total of three specimens. On the other hand *Phlyctaenaspis* is well represented in the con-

207 The *Coccosteus* material may prove to include several generic types; Gross, for example, has recently pointed out that one described as "*Coccosteus*" from the Portage is *Leptosteus* of Wildungen.

208 Skrifter om Svalbard og Ishavet **22**, **23**, Oslo, 1929.

tinental deposits at Campbellton, and at Bear Tooth Butte there are abundant acanthaspid remains in a seemingly fresh-water deposit.

To sum up: In the Lower Devonian of America primitive arthrodires are found in both fresh-water and, to a lesser extent, in marine beds. Later both the remaining primitive forms as well as almost all other advanced or specialized types are found exclusively in marine deposits. This trend is indcative of a fresh-water origin for the arthrodires, but also of a strong seaward movement in the Lower Devonian, followed by a rapid marine radiation of the group.

The European evidence appears to us to be in accord with this view. Primitive arthrodires are found there in the Lower Devonian both in the "Old Red" phase in Spitzbergen and in the upper part of the marine Lower Devonian in the Rhineland. Except for *Coccosteus* arthrodires are rare in the later "Old Red" phase, but common and varied in the marine beds of the later Devonian; *Dinichthys* and other giant types are practically unknown, but a host of wierd forms are present in the marine Wildungen beds of Germany.

Acanthodians.—The small sharks of the Order Acanthodii, characterized by strong fin spines and by scales and skeletal structure of bone-like nature, appear to have been essentially fresh-water forms throughout their history. The only complete American specimens (pertaining to the genera *Cheiracanthus, Climatius, Acanthoëssus* and *Diplacanthus)* are found in seemingly fresh-water deposits in the Lower Devonian at Campbellton and the Upper Devonian of Scaumenac Bay. Spines of the genus *Onchus,* usually attributed to this order, are present at two horizons in the Silurian of Perry County, Pennsylvania, in beds which seem to be of continental origin, in the Lower Devonan at the Knoydart, Campbellton, and Bear Tooth Butte localities under apparently similar conditions, and in the "Catskill" of New York, in a seemingly deltaic deposit. The only suggestions of a marine environment for acanthodians are given by the report of fragmentary material referred to this group from three New York black shales (Marcellus, Genessee conodont bed, Rhinestreet). In the last two of these we are apparently not dealing with strictly marine conditions.

Although it is possible that some of the many types of "shark" spines characteristic of Paleozoic marine deposits may have pertained to acanthodians, this is not certain. Very likely the acanthodians (in a broad sense) may be ancestral to the marine "sharks" to which many of these spines pertain; but it will be noted that none of these spine "genera" is found in the Silurian, and with the assumption of descent from fresh-water acanthodians we may also reasonably assume a migration from fresh to salt waters.

The absence of remains of spiny sharks in the Silurian otherwise than in the form of isolated spines may be due, we suggest, to the fact that like the anaspids they may have been, to start with, inland dwellers which tended downstream and, in their possible "shark" descendants, out to sea in the early Devonian. The comparative rarity of these forms later than the early

Devonian [209] may be due to the irruption of higher bony fishes, more highly organized forms of similar body build and very probably, in many cases, of similar habits.

Ichthyodorulites.—Under this heading we may group most of the isolated types of shark spines not uncommon in the Devonian. *Onchus* we have noted as a probable acanthodian; *Ctenacanthus* is a cladoselachian. The numerous shark spines of other genera listed are in general of uncertain affinities. In the lower Devonian almost all of the finds of ichthyodarulites are in seemingly fresh-water deposits. Later and more abundant Devonian finds are almost without exception in deposits of marine nature. This suggests a migration from fresh to salt waters and agrees with the hypothesis that the essentially fresh-water acanthodians are close to the line of ancestry of later "shark" groups, many of which retain spines on part, at least, of the fins.

Miscellaneous "shark" types.—Apart from spines or types definitely assignable to recognized "shark" orders, such as the acanthodians and cladoselachians, the American Devonian material includes a number of generally obscure and incompletely known forms which appear to be "sharks" in a broad sense of that term. In the lower Devonian such miscellaneous material includes only teeth upon which the genera *Protodus* and *Doliodus* are based, from the presumed fresh-water beds of Campbellton. The later middle and upper Devonian types appear in deposits which are all presumably of salt-water origin. Of these later forms *Onychodus* is the most abundant and widespread, occurring in numerous marine formations from the Onondagan on into the upper Devonian. This form is represented by bony jaw plates bearing pointed teeth, and especially by whorls of large curved symphysial teeth; various plates and large scales are more doubtfully assigned to this genus. The sytematic position of *Onychodus* has long been a problematical one. Because of the presence of bone it has usually been considered in the past a crossopterygian. But in other respects it shows no similarities to this group. Although the symphysial teeth suggest certain paleozoic "shark" types, the assignment to the chondrichthyans of a form possessing bone was long repugnant. But, as noted below, the descent of the now boneless sharks from armored ancestors is a hypothesis for which there is increasing evidence, and Smith Woodward's suggestion that the marine *Onychodus* is an offshoot of the essentially fresh-water acanthodians is a not unreasonable one.

Macropetalichthys is known only from the bony skull roof and the underlying braincase; there is no definite association of teeth, jaws or post-cranial material. It has in the past been assigned, because of its armor, to the arthrodires. But the nature of this armor shows no resemblance to that of true arthrodires. Stensiö has show that the braincase is essentially elasmobranch in nature, and it seems likely (as supported by evidence from several other genera) that *Macropetalichthys* represents a transitional group (Stegoselachii) between primitive armored forms and the later purely cartilagenous sharks.[210]

---

209 *Acanthodes* is however locally abundant in the Permian of Germany.

210 During a revision of this manuscript, this theory has been completely confirmed by the description by Broili (S. B. Bayer. Akad. Wiss., Dec. 1933, pp. 417-437) of a shark-like skeleton of a macropetalichthyid from the Hunsrück.

The genus appears to be a marker for Onondagan time, being found only in marine strata of that age, where it is not uncommon. *Asterosteus* is a second and rarer type of "shark" braincase retaining some traces of an armored roof; it is apparently close to the peculiar *Gemundina* of the German Devonian, and is known only in the Onondagan of Ohio and (questionably) New York.

In several middle and upper Devonian deposits in New York State are reported two-pronged teeth assigned to the genus *Dittodus (Diplodus)*. These teeth are of the type found in the pleuracanth sharks of the later coal swamps and lower Permian fresh-water beds. The Devonian finds of such teeth include only one citation from the Hamilton and two from the Genesee, salt-water deposits with, however, possibilities of fresh-water admixture in the latter group. No trace of the very characteristic and readily preserved pleuracanth spines has been found in association, and it is not improbable that teeth of this sort may have been present among other poorly known Devonian "shark" groups. *Phoebodus* is a generic form including three-pronged teeth, recorded from the Cleveland shale and the Cedar Valley limestone of Iowa. These teeth might pertain to cladoselachians, to pleuracanths, or to some other group of early "sharks." *Xenodus (Goniodus)* includes some small teeth of problematical nature from the Huron shale.

In *Orodus* (in the Genesee conodent bed) and *Eoörodus* (Upper Devonian of Missouri) we have the first member of the marine true sharks of the heterodont-hybodont group not uncommon in the Carboniferous; in *Helodus* (Upper Devonian, Missouri and Alberta) and a questionable *Psammodus* (from the Onondagan) the forerunners of the true pavement-toothed marine "sharks" of the Carboniferous (the bradyodonts of Smith Woodward).

The array of varied "shark" material considered in this section is almost entirely marine in nature, and almost entirely from the Middle and Upper Devonian; the situation parallels that of the record of "shark" spines noted above.

Cladoselachians.—The *Cladodus* type of tooth, with a long central cusp and smaller lateral ones is common in the marine Carboniferous. In the Cleveland shale this tooth type is found present in the jaws of the dominant "shark," *Cladoselache*, and also associated with sharks bearing spines of the *Ctenacanthus* type but otherwise similar to the last-named genus. *Cladodus* teeth and *Ctenacanthus* spines are widespread in salt-water deposits of the Upper Devonian; both are present but rare in the marine Middle Devonian. The cladoselachians are thus marine throughout their known history. The presence of spined as well as spineless types within the group is at least suggestive of acanthodian descent.

Shark-like fishes—general.—If we summarize the evidences of distribution of early chondrichthyan given in the four preceding sections, the following facts seem clear: (1) fresh-water acanthodians are present from Silurian times on; (2) other "shark" types (not common) in the American Lower Devonian are almost entirely from fresh-water localities; (3) numerous and varied "shark"types were present in the seas in the Middle and late Devonian but are almost unknown in continental deposits formed at that time.

Have the chondrichthys originated in the seas, where lay their main center

of distribution from Middle Devonian times on, or in fresh waters? If we, orthodoxly, assume a salt-water origin for these forms which dwell almost exclusively in the seas today, we encounter difficulties. We must, first of all, attempt to explain away the fact that the acanthodians, first of shark groups to enter the scene, are essentially fresh-water forms. To meet this objection it may be argued that the acanthodians were a side branch which migrated into fresh waters. But then there is encountered a further perplexing question: where are the marine sharks from which these Silurian and early Devonian continental forms came? They are not known; hence it must be assumed they were entirely soft-bodied and lacking the hard teeth and spines which are later found plentifully to represent the "sharks" in marine deposits. But this drives us to the absurd conclusion that the teeth and spines of the early acanthodians were developed independently of the similar structures in the later marine sharks, and also forces us to overlook the fact that a number of Devonian marine sharks (as *Macropetalichthys)* were somewhat armored, as were the early acanthodians.

On the other hand, a hypothesis which suggests an origin of marine "sharks" from acanthodians (in a broad sense) fits many of the known facts of the case. The structure of *Acanthodes* of the Permian shows a number of peculiarities which would debar this genus from a position ancestral to later sharks; but it seems highly probable that the inadequately known Devonian acanthodian genera will upon further study reveal forms close to the stem of later selachians.

Bony Fishes—general.—That the higher fishes, the Osteichthys, including crossopterygians, lungfish and actinopterygians, were primarily fresh-water types is generally conceded on structural grounds. Lungs appear to have been primitively present in all three major groups. They are still present in living lungfishes; the entirely extinct crossopterygians, as the presumed ancestors of the tetrapods, must have possessed them; and the recognition that the living African genera *Polypterus* and *Calamoichthys,* which have functional lungs, are not crossopterygians but the descendants of the Palaeozoic palaeoniscids indicates that the actinopterygian air bladder was originally a lung. Recent studies on fish kidneys (Homer W. Smith) also indicate the fresh water origin of the group.

The lack of an adequate fresh-water component in the Middle Devonian of North America prevents any confirmation of this thesis by the data here assembled. The Osteichthys appear on the paleontologic stage in the Middle Devonian with dramatic suddenness. In the entire Lower Devonian the known remains of this group include but two specimens of lungfish tooth-plates from North America and a few scales and other fragments of a presumed crossopterygian *(Porolepis)* in the Rhineland. In the Lower "Old Red" sandstone of the dominant types were ostracoderms, primitive arthrodires and spiny sharks. In the succeeding Middle "Old Red" (Orcadian), without any appreciable change of environmental conditions, these groups have almost disappeared and their places have been taken in great measure by a host of higher fishes—mainly crossopterygians, with lungfish and primitive actinopterygians *(Cheirolepis* and *Stegotrachelius)* in lesser numbers.

Whence do these Middle Devonian bony fishes come? They are obviously not newly evolved, for the three major groups are already quite distinct from one another, although closer than at later times. It has been suggested that their appearance at this time is due to migration from some other continental area. It would appear to us, however, that there is another possibility—that their early history may have taken place in the upper reaches of river systems. Their appearance on the scene at this time may be due to a down-stream migration or rather perhaps (with the same result) due to the marine transgression of the Middle Devonian, which tended to bring shorelines and areas of deposition closer to the regions inhabited by these fishes. It is interesting to note that the bony fishes are the third of a series of slim-bodied, active fishes which swim onto the scene in successive stages of our story—anaspids (Upper Silurian), acanthodians (Lower Devonian), bony fishes (Middle Devonian). In no case is there any considerable amount of material of these groups from starta older than that of their major appearance, and yet all are highly developed when first seen. In all these three cases the origin of the group in the faster currents of the higher reaches of river systems is a hypothesis which also seems to agree with the known facts.

Almost no traces of bony fishes are to be found in the marine Middle Devonian of Europe. This same paucity of osteichthyan material is seen in the marine beds which furnish most of the vertebrate faunas in the North American Middle Devonian; they contain, of these groups, only a few *Dipterus* tooth plates. The few continental finds give us the oldest recorded American crossopterygians.

In the Upper Devonian all three bony fish groups are well represented in North America.

Crossopterygians.—The Crossopterygii are obviously centered in fresh waters. *Eusthenopteron,* known only from Scaumenac Bay (fresh-water), but very abundant there, is the best known American form. *Diplopterax, Glyptolepis* and *Osteolepis* are cited in the "Old Red" of east Greenland. *Sauripteris* and*Glyptopomus* are present in "Old Red" types of deposit in New York (?) and Pennsylvania. *Holoptychius* is represented mainly by scales, which are reported at some two dozen localities, mainly in New York and northern Pennsylvania. Most of the records are from typical "Old Red" deposits without any suggestion of marine conditions; the remaining ones are associated with marine fossils, but geographically come from the edge of the "Catskill" delta. It seems reasonable to assume that this form was a stream-dweller, remains of which would occasionally have drifted out of the delta into adjacent waters.

There is no reason, on the basis of American material, for us to disagree with the general conclusion that the crossopterygians had their evolutionary center in fresh water.

Lungfish.—Of all the higher fish groups, one would *a priori* imagine that the Dipnoi would present the most consistent picture of a purely fresh-water group. The living lungfish are purely stream and lake dwellers, and their well-developed lungs seem closely correlated with existence in interior regions subject to seasonal drought. But the early history of the group, as indicated

by such evidence as we have here collected, shows that the reverse is really the case.

Lungfishes *(Dipterus* and *Scaumenacia)* are found at a number of Upper Devonian localities which are presumably fresh-water in nature, and even in the Lower Devonian we find a *Dipterus* tooth associated with land plant materials at Bear Tooth Butte. Certain other Upper Devonian specimens, particularly of *Dipterus* and *"Ctenodus"* occur in salt-water deposits, but under conditions where some incursion of remains of fresh-water animals is not impossible.

On the other hand we find throughout the Devonian *Dipterus* teeth present in marine limestones, associated with an abundant fauna of corals and other forms indicative of typical marine conditions, and present, in such instances as the Upper Devonian of Iowa, in such numbers as to exclude any possible explanation of their presence as "strays." *Dipterus* is in Iowa accompanied by *Synthetodus,* a type of tooth plate which Eastman believes to be a modification of the dipnoan pattern (but which Hussakof and Bryant consider to pertain to a "shark").

As far as we are aware, there is little indication of a persistence of lungfish in marine waters beyond the Devonian. This short inroad of a typical continental group into the sea may find its explanation in a consideration of lungfish feeding habits. The dipnoan tooth plate is adapted for crushing small invertebrates. There was a wealth of suitable food in the Devonian seas for any form with teeth capable of coping with shells, and it would seem that the lungfish, although not otherwise particularly adapted for marine life, found here an ecological niche into which, for the time, they fitted fairly well. Toward the end of the Devonian there appear arthrodires with crushing teeth and then the earliest of the pavement toothed sharks so common in the Carboniferous; the development of this last group seems to have terminated the marine career of the lungfish.

Actinopterygians.—*Cheirolepis* and *Stegotrachelis,* oldest of ray-finned fishes, are present in the middle "Old Red" of Scotland; no palaeoniscid material is reported, on the other hand, from the dominantly marine middle Devonian of North America (or the Rhineland strata of this age). This is in keeping with the presumed fresh-water origin of the Actinopterygii. In the Upper Devonian of North America *Cheirolepis* is found in fresh waters at Scaumenac Bay. The group is not represented in the "Catskill" deposits of New York and Pennsylvania, but this may be due to the fact that it is much easier to overlook the tiny scales of palaeoniscids than the much larger scales of *Holoptychius* or the heavy plates of *Bothriolepis,* the two forms whose remains comprise most of the "Catskill" finds.

There is a considerable number of reports of palaeoniscid material from various black shale deposits in the Upper Devonian. These have been generally assigned to *Rhadinichthys* or, earlier, *"Palaeoniscus"* (a Permian genus) but may, as Smith Woodward has suggested in one case, be better assigned to the recently erected "Old Red" genus *Stegotrachelus.* Some of these black shale finds are reported under circumstances which render a fluviatile origin of the cadavers reasonable. On the whole, however, the evidence suggests

that the actinopterygians were venturing into salt waters, a beginning of the marine trend seen so strongly in the Mesozoic ray-finned types.

The faunal contrast between groups.—It was noted at the outset that the evidence for the fresh-water nature of any deposit is chiefly of a negative nature and hence difficult to maintain for any single locality. But the group-by-group discussion above shows that there is strong internal evidence for the distinctions here claimed between fresh and salt water deposits.

If in the Upper Devonian, the faunal list from such presumed fresh-water beds as those of Scaumenac Bay, East Greenland, and the "Catskill" reds be compared with that of the definitely marine formations, such as the black shales of western New York, and Ohio, we find an extreme contrast in faunal content, not merely in genera or species, but in major groups. In the presumed fresh-water beds at least 95% of the material consists of antiarchs (mainly *Bothriolepis*), crossopterygians (as *Holoptychius, Eusthtenopteron*) and lungfish (as *Scaumenacia*); the remaining materials included two arthrodires (one the ubiquitous *Coccosteus*), a palaeoniscid (*Cheirolepis*), an acanthodian, a cephalaspid, two heterostracans and a questionable anaspid. In the black shales, on the other hand, more than 95% of the material consists of sharks unknown in the presumed fresh-water localities and a huge array of arthrodires which, except for the rare *Coccosteus*, are quite unknown in the presumed fresh-water beds. Other remains included only lung-fish teeth apparently distinct from fresh-water types and one or two actinopterygian genera, unknown in presumed fresh-water beds. If it is assumed that certain deposits which we maintain to be continental are in reality marine sediments, in which invertebrates chanced not to be present, or preserved, we are driven to the untenable conclusion that there existed two contemporary but almost absolutely distinct marine fish faunas which never mixed!

The same is true of the contrast between the faunas of the marine deposits of the Onondagan, Hamilton, and the Rhineland Middle Devonian, and the presumed continental Middle "Old Red" of North Scotland and the Orkneys (almost unrepresented in North America). The marine beds include mainly arthrodires of varied sorts and peculiar "shark" types. The "Old Red" on the other hand is very rich in crossopterygians and almost destitute of arthrodires, (except *Coccosteus*) and of sharks except for acanthodians, of which no typical examples are found in the marine strata.

In the lower Devonian the contrast is not so great, either in America or Europe; particularly among pteraspids and primitive arthrodires we find many common elements in both marine and presumed continental beds; we seem to have a period of transition.

In the Silurian we find but a single fauna present, and never is there a faunal assemblage in any typical marine bed. The presumed fresh-water nature of Silurian beds containing any considerable amount or variety of vertebrate material is confirmed by the general agreement that the fauna is essentially similar to that of the lower "Old Red,"[211] rather than the definitely marine phases of the lower Devonian. In case after case we find in Europe and North America Downtonian (and lower "Old Red") fish faunas associated

211 In fact, the argument for the inclusion of the Downtonian in the Devonian is in great measure based on this similarity.

with eurypterids, ceratiocarids, plants (in the lower Devonian), possibly *Leperditia*, but only rarely invertebrates of any other sort—a fauna which can by no stretch of the imagination be called typically marine and which seems to us highly suggestive of fluviatile conditions.

Analysis of the faunal content of the various deposits thus tends to show that our claims for the fresh-water nature of many of them finds strong justification in the distinctions found between their faunas and those of known marine beds.

Conclusions

The first sections of this paper were devoted to a summarization of all available evidence concerning the habitat of the early vertebrates to be obtained from North American pre-Carboniferous finds.

In the preceding discussion this material has been analyzed both as a whole and by a more detailed consideration of the evidence regarding the various fish types concerned. As has been seen, this analysis strongly suggests that fresh-waters were the early center of fish history. The evidence is in accord with the following series of hypotheses:

(1) That the earliest vertebrates (presumably agnathous "ostracoderms") were entirely inhabitants of fresh waters in Ordovician times.

(2) That the "ostracoderms" remained essentially fresh water forms to the end of their history in the Devonian, although there was some tendency toward a marine life in the Heterostraci.

(3) That the placoderms were of fresh water origin, but that while the anitiarchs remained almost entirely in fresh waters, the arthrodires in the lower Devonian migrated in the main into the seas, where the greater part of their short but remarkable evolutionary history took place.

(4) That the shark-like fishes originated in fresh waters, where the typical acanthodians, oldest of known "shark" groups, remained to the end of their history, but that here, again, a strong trend toward the sea took place at about the beginning of the Devonian; the oceans were the center of shark history from that time on.

(5) That the higher bony fishes had their origin in fresh waters, in which their evolutionary center remained throughout the Devonian; but that the actinopterygians showed an early tendency toward the seas in some instances and that the lungfish, while persistently fresh-water forms as a group, developed a short-lived marine side branch in Devonian times.

We make no claim that the body of facts here presented furnishes positive proof of these hypotheses; such proof is, from the nature of the case, impossible. On the other hand we believe the facts assembled here render untenable the converse hypothesis of vertebrate marine origins. A consideration of selected portions of the evidence might permit of such an interpretation; but examination of the entire body of facts derivable from the American fossil record leads unmistakably to the conclusion that the early vertebrates were dwellers in fresh water.

MUSEUM OF COMPARATIVE ZOOLOGY,
HARVARD UNIVERSITY,
CAMBRIDGE, MASS.

THE UNIVERSITY OF CHICAGO,
CHICAGO, ILL.

TABLE 1

To show the environment under which specimens of the vertebrate genera are reported at various Silurian and Devonian horizons in North America. The numbers represent the presumed varying environmental conditions under which deposition of the rocks containing the remains took place, ranging from 1 = presumably fresh water, to 4 = typical marine occurrences (see text). Each number represents the report of a genus from a single formation, the number of citations giving a rough suggestion of relative abundance. Attention is called to the fact that fresh-water beds of Middle Devonian age are very rare in North America and that hence our picture of the vertebrate life of that time is necessarily incomplete.

	Silurian	L. Devonian	M. Devonian	U. Devonian
AGNATHA				
Heterostraci				
Thelodus	1	4		
Cyathaspis	111			
Palaeaspis	11222			
Pteraspis		1		
Protaspis		1		
Cryptaspis		1		
Glossoidaspis		4		
Cardipeltis		14		
Cyrtaspis		1		
Psammosteus		1		2
Phyllolepis				144
Anaspida				
Ctenopleuron	1			
Euphanerops				1
Osteostraci				
Cephalaspis		111	1	1
PLACODERMI				
Primitive				
Arthrodires				
Phlyctaenaspis		1		
Anarthraspis		1		
Euryaspis		1		
Camptaspis		4		
Acanthaspis			44	3344
Indeterminate		4		
Advanced				
arthrodires				
Coccosteus			144	1112344
Groenlandaspis				1
Leptosteus				4
Dinichthys			444444	2334444444444444
Aspidichthys			444	234444
Holonema			44	1222334444444
Protitani'thys			44	
Titanichthys				4
Dinomylostoma			4	3444

TABLE 1 (Continued)

	Silurian	L. Devonian	M. Devonian	U. Devonian
Stenognathus				34
Perissognathus				3
Copanognathus				3
Selenosteus				344
Callognathus				444
Stenosteus				44
Hussakofia				4
Mylostoma				44
Machaerognathus				3
Diplognathus				4
Dinognathus				4
Trachosteus				4
Ptyctodonts				
Palaeomylus			4	334
Deinodus			4	
Rhynchodus			4	34444444
Ptyctodus			4444444	3344444444
Antiarchi				
Asterolepis				1
Remigolepis				1
Bothriolepis			11	11111111222
CHONDRICHTHYES				
Acanthodii				
Onchus	22	11	1	2
Cheiracanthus		1		
Climatius		1		
Acanthoëssus		1		13
Diplacanthus				1
Indeterminate				1
Misc. "Sharks"				
Protodus		1		
Doliodus		1		
Macropetalichthys			44444	
Asterosteus			44	
Onychodus			44444444	334444444
"Dittodus"			4	334
Phoebodus				44
Xenodus				4
Shark Spines				
Pinnacanthus		1		
Helenacanthus		1		
Gyracanthus		1	4	1233444
Bulbacanthus		1		
Homacanthus		1		
Machaeracanthus		14	114444	34

TABLE 1 (Concluded)

	Silurian	L. Devonian	M. Devonian	U. Devonian
Gamphacan'us			4	444
Cyrtacanthus			44	
Eczematolepis			44	34
Oestophorus				344
Acmoniodus				3
Anodontacan's				3
Stethacanthus				34
Atopacanthus				444
Hoplonchus				4
Cladoselachii				
Cladodus			4	334444
Ctenacanthus			44	334444
Cladoselache				4
Monocladodus				4
Elasmobranchii				
Eoörodus				4
Orodus				3
Bradyodonti				
Helodus				44
Psammodus?			4	
OSTEICHTHYES				
Dipnoi				
Dipterus		14	4444	123333444
Synthetodus				234
Ctenodus				122234
"Conchodus"				4
Palaedaphus				23
Ganorhynchus				3
Scaumenacia				1
Crossopterygii				
Holoptychius			1	1111111111111222222
Holoptychius				3334
Sauripteris			1	11
Glyptopomus				1
Eusthenopteron				1
Diplopterax			1	
Glyptolepis				2
Osteolepis				2
Actinopterygii				
Rhadinichthys				33344
Tegolepis				4
Cheirolepis				1
Indeterminate				4

TABLE 2

Summary of the citations of table 1. In A the four classes of deposits given in table 1 are retained to show the total of generic citations in each of them at various horizons. In B the material is grouped to show the percentages of generic citations for essentially fresh-water localities (classes 1 and 2) and essentially marine (classes 3 and 4).

A

	Class 1 (Fresh)	Class 2	Class 3	Class 4 (Marine)
Silurian	7	5	0	0
L. Devonian	26	0	0	8
M. Devonian	10	0	0	62
U. Devonian	43	23	51	116

B

	% fresh	% marine
Silurian	100	0
L. Devonian	77	23
M. Devonian	13	87
U. Devonian	29	71

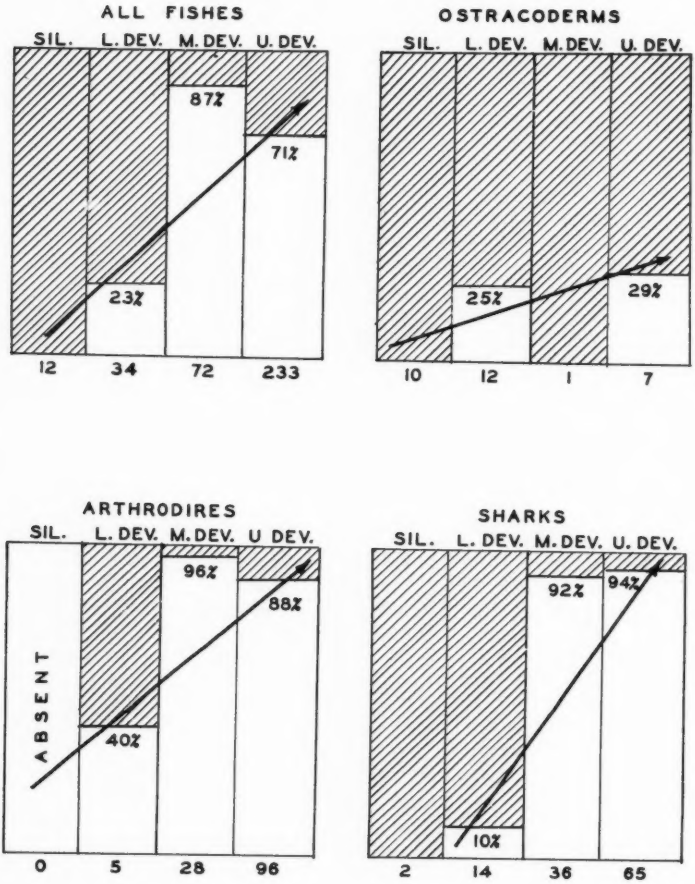


Fig. 2. Diagrams to show relative citations of members of various groups in presumed fresh and salt water deposits in Silurian and Devonian times. The rarity of American continental deposits presumably shifts the balance overmuch toward the marine side in the Middle Devonian. The figures below each column indicate the number of generic citations available. Fresh water hatched; marine blank. Arrows indicate varying trend toward marine environment.

SUMMARY OF UPPER DEVONIAN STRATIGRAPHY [1]

GEORGE H. CHADWICK

The Upper Devonian terrane of New York and adjoining regions consists of many thousands of feet of clastic deposits, in the east or southeast, thinning down to but a few hundred feet at the west or northwest. Beds which are coarse sandstones, or conglomerates, at the east, grade westward into shales that grow continually finer until at length they become black and extremely fissile. Beginning even in the Middle Devonian (the Hamilton) and continuing throughout the Upper Devonian, moreover, continental red-beds were laid down contemporaneously with the marine sediments, always on the landward or eastern side of the latter, but reaching ever farther and farther west as deposition progressed. It is these red-beds loosely called "Catskill" that are looked upon as the great repository of fish remains; but it is the absence of other fossils rather than the actual abundance of fishes that has given them this reputation, for at the other remote extreme, in the black shales of Ohio, remains of fishes vie with or exceed in abundance those of these continental strata.

A. Continental deposition began in the lower *Hamilton* of the Hudson Valley. To the Hamilton red-beds of Greene, Albany, Ulster and Schoharie counties, New York, the name *Kiskatom* formation is now applied, pending the time when this mass may be more accurately subdivided. The original Catskill formation of Mather included all of the Kiskatom (about 2500 feet thick, including the Tully) and perhaps a little of overlying beds of Genesee age. But since later workers extended the name Catskill to the five thousand feet of still higher similar beds in these Catskill mountains, and since *Catskill* has later come to be restricted to these higher beds which are of Upper Devonian age (falsely supposed to be supra-Oneonta), it may be best to let the name Catskill continue in this later significance (covering Genesee-Naples equivalents), excluding from it the Mid-Devonian Kiskatom strata. Westwardly, the Kiskatom passes into the familiar marine beds, the Skaneateles, Ludlowville and Moscow of the Hamilton group.

B. The rocks composing the *Genesee* group are typically dark to black shales, in western New York. All told, they include four members, namely (2) Geneseo black shale (see the correlation chart, Figure 1), (3) Genundewa limestone, (4) West River dark shale, (5) Standish flags. From Canandaigua lake eastward, these are underlain bv the (1) Tully limestone, whose pertinence to Upper Devonian is now disproved. Westward, this limestone goes out of the section, the (2) Geneseo being then bottomed by a seam of fossiliferous pyrite wrongly called "Tully" and itself in turn gradually pinching out

[1] Written primarily to supply a stratigraphic background for the paper by Romer and Grove, in the same number of the American Midland Naturalist; hence the reference to fish faunas.

until on lake Erie the (3) Genundewa limestone and (4) West River black shale alone are left, save that just beneath the Genundewa is a thin "conodont" bed containing annelid and fish remains.

East of Canandaigua, the (5) Standish thickens rapidly, are does also the (4) West River as it grows more sandy. On Seneca and Cayuga lakes, these two have become the *Sherburne* flagstone formation, while at Sherburne itself even the (2) Geneseo and (1) Tully have changed into essentially a part of the type (1-5) Sherburne. Still farther east, the whole mass becomes red and then constitutes a lower half of the restricted (i.e., Upper Devonian) Catskill.

C. Above the Genesee group, on Canandaigua lake, is the *Naples* group *as defined originally* by J. C. Clarke. This there consists of four members, namely (6) Middlesex black shale, (7) Cashaqua olive shale, (8) Rhinestreet black shale, (9) Hatch dark shales. These four are traceable without difficulty to lake Erie, decreasing in thickness and the Hatch assimilating with the Rhinestreet into the (8-9) Attica black shale (mistakenly "Rhinestreet").

Eastward, the Middlesex-Cashaqua become the (6-7) *Ithaca* formation (recently analyzed into subdivisions by Caster), while the Rhinestreet-Hatch beds pass into the (8-9) *Enfield* formation. In turn, the Ithaca splits into the (6) Otselic shale and (7) Cincinnatus flags, the latter becoming almost at once the continental (7) *Oneonta* red-beds. [The type Oneonta probably absorbs also the (6) Otselic.] The Enfield likewise splits, into the (8) Kattel ("Leiorhynchus globuliforme") zone and the (9a) Juliand and (9b) Van Etten ("First Tropidoleptus") zones. The Kattel persists as a marine deposit (600 feet thick) far east between Oneonta reds below and red Enfield beds above, and forms a recognizable band of gray flagstones clear through the continental mass of the Catskill mountains. The continental Kattel and later beds, of Enfield age, constitute the (8-9) *Katsberg* red-beds formation or upper half-mile of the restricted Catskill, while the lower half-mile, of Sherburne-Ithaca age, is the before-mentioned (1-7) Onteora red mass, including at its top the true Oneonta formation. These names Onteora and Katsberg are respectively the Indian and the Dutch correct cognomens for the mountains miscalled Catskills by the English.

D. The Enfield beds of the Naples group are followed directly by those of the *Chemung* group. The very fossiliferous Chemung strata are commonly divided into the *Cayuta* formation below and the Wellsburg formation above, but farther west, where these strata compose the upper portion of what is familiarly known as the "Portage (correctly Nunda) group," a greater refinement is possible. There, on the Genesee river, the members are seven in numbr, namely (10) Grimes sandstone, (11) "Gardeau" shale (as finally restricted), (12) Table Rock sandstone, (13) Letchworth (Hall's Portage and most of Clarke's "Gardeau") shale, (14) Portage (incorrectly "Nunda") sandstone or bluestone, (15) Pipe Creek black shale, and (16) Hanover olive shales. Commonly on the Genesee, the last two have ben combined as the (15-16) Wiscoy shale, while the name "Gardeau" has covered (11) to (13). But Hall's original Gardeau was (8) to (11), and Clarke's first restric-

tion of the term was to (8) and (9)—the Attica or Enfield, of the Naples group.

From the Genesee river westward, this Chemung group thins rapidly and loses its sands, becoming on lake Erie the olive (10-14) Angola shale, overlain still by the (15) Pipe Creek and (16) Hanover. But eastward there are striking changes. On Canandaigua lake the Chemung brachiopod fauna has entered the (10) Grimes and the (14) Highpoint (Portage) sandstones. The (15-16) Wiscoy shale has altered to the (15-17?) Prattsburg sandstone, and it is the Highpoint and Prattsburg that soon eastward become the (14-16) Wellsburg sandstone or upper Chemung. The (11-13) Westhill ("Gardeau") shale similarly passes into the main mass of the (10-13) Cayuta shale or lower Chemung, while the (10) Grimes sandstone is the (10) Danby ("Dalmanella danbyi") zone at the base of Cayuta.

Continuing east, but mostly in Pennsylvania, the Wellsburg sandstones become the *Montrose* red-beds (of Vanuxem, not White), while in New York the Cayuta shales soon afterward also turn red, receiving the name *Catawissa* red-beds from a locality farther south, in Pennsylvania, on the opposite side of the geosyncline. Of these Chemung rocks, only the Cayuta or Catawissa reds appear to be represented east of the Delaware rivr, in New York, and these only on the higher lands, rising rapidly to the mountain tops and being present in the Catskills proper only as the white (10) Slide Mountain conglomerate capping the highest peak alone.

In eastern Pennsylvania, the type *Pocono* sandstone (and white conglomerates) appears to be a similar development of some, or all, of the Chemung strata. Fieldwork is needed.

E. The fossiliferous strata formerly called "Chemung" on the Genesee river are now known to differ in the presence of one hundred thirty species not found in the true Chemung strata below, and in the absence of two hundred forty species (including many characteristic forms) of the typical Chemung fauna, while there are less than a hundred species in common. These beds, with the "Athyris angelica fauna" constitute the *Canadaway* group, which, traced eastward, goes wholly above the type Chemung. On Lake Erie, the Canadaway is readily subdivided as follows: (17) Dunkirk black shale, (18) Gowanda (formerly Portland beds, preoccupied), (19) Laona sandstone, (20) Westfield shale, (21) Shumla sandstone, and (22) Northeast shale, I. C. White's "Portage."

The (17) Dunkirk is easily followed to the Genesee river, east of which it becomes mostly light-colored and passes into the (17) Canaseraga sandstone, and apparently at length includes the Fall Creek conglomerate capping the Chemung group. The continental phase of the Dunkirk is known at Towanda creek "narrows," perhaps in the "Pocono" at Tunkhannock. The (18) Gowanda is identified on the Genesee river as the (18) Caneada shale, becoming the Mansfield (partly) "red" beds of Pennsylvania and the fully red Blossburg beds (of Conrad) a little farther southwest. [Recent fieldwork makes the Mansfield, and at least some of the Blossburg, (17) Dunkirk.]

The (19) Laona and (21) Shumla sandstones are not so easily traced.

Apparently, they give way to shales across northern Cattaraugus county, New York, but later resume as the (19-21?) *Rushford* sandstones on the Genesee, which finally form part of the so-called "Cattaraugus" reds aroundKnoxville, and of the "Oswayo" around Mansfield and Blossburg, Pennsylvania.

(22) barren Northeast shales become the fossiliferous (22) Machias beds before reaching the Genesee, and on that river have furnished some of the best known collecting grounds for "Chemung" (i.e., Canadaway) fossils. They go into the continental facies on crossing into Pennsylvania (Tioga county), are a part of the "Cattaraugus" at Knoxville, and are the "Mauch Chunk" and part of the "Oswayo" at Mansfield and Blossburg, Pennsylvania.

Eastward, the Pottsville conglomerate laps all of these out before reaching Towanda mountain, where the Gowanda is next beneath it and is mistaken for "Pocono."

F. The *Conneaut* group, or lower Chagrin has been named for the exposures on Conneaut creek, in Ohio and Pennsylvania, which crosses the two members of the group present on lake Erie, namely the (24) *Girard* shale and the (25) *Chadakoin* beds, I. C. White's "Chemung." But from Cattaraugus county, New York, eastward, the (23) *Cuba* sandstone enters at bottom of the group. Moreover, in eastern Cattaraugus county, the base of the (25) Chadakoin, there called "pink rock" by the drillers, contains the Hinsdale sandstones. Across New York, the barren (24) Girard shale is replaced by the fossiliferous (24) Volusia shale, which shows reddish color and iron-ore seams before reaching the Genesee river and assumes the continental phase in southeast Allegany county, New York, and Potter county, Pennsylvania. The "pink rock" reddish interfingerings in the (25) Chadakoin reach as far west as its type locality, Jamestown on Chautauqua lake, but the full red-beds facies is not attained short of Allegany county, New York, while in Potter and Tioga counties, Pennsylvania, it is mistaken for "Oswayo" and is then bevelled out beneath the Pottsville, west of the Tioga river.

G. The *Conewango* group, upper Chagrin, completes the known Upper Devonian succession in this region, and is confined to its western part. In Allegany county, New York, it is known as the *Cattaraugus* and *Oswayo* formations, the former partly red (continental). In northwest Pennsylvania, where it is all marine and fossiliferous, it is divisible into (26) LeBoeuf sandstone or the Panama conglomerate of New York, (27) Amity shale, (28) Millers sandstone, (29) Saegerstown shale and (30) Woodcock sandstone, these five constituting the "*Venango* group" overlain by the (31) Riceville shale. At Warren, Pennsylvania, the Conewango formation is supposed to comprise strata equivalent to all these, but they have not been exactly individually determined, nor has the detailed correlation with the Cattaraugus-Oswayo been satisfactorily accomplished. Within the Cattaraugus there are (a) a basal, Wolf Creek, conglomerate, possibly the (26) Panama, (b) lower shales, perhaps the (27) Amity, (c) a middle, *Salamanca*, conglomerate or Mount Hermon sandstone, possibley the (28) Millers, (d) higher shales, perhaps (29) Saegertstown and included in these shales a third,

Tunangwant or "Killbuck" conglomerate not so easily identified with the (30) Woodcock. Nor is the Oswayo clearly equivalent to the (31) Riceville. It is even likely that the Woodcock and Riceville are here absent. Only the lower Cattaraugus extends as far as eastern Potter county, Pennsylvania, being there included in the top of the Oswayo of Fuller (not Glenn), a continental mass of "Pocono" facies. The Oswayo of Glenn (not Fuller), Flatiron of Caster, which is marine and fossiliferous, goes no farther east than western Potter county, since the Pottsville conglomerate bevels down across these higher beds of the Upper Devonian from Olean, New York, eastward.

In general, then, we see a progressive loss of the top beds from west to east, by pre-Pottsville (summit) erosion, so that the highest remaining member at the extreme east is of the Chemung group (Pocono of the Pocono mountains in Pennsylvania, Slide Mountain of the Catskill mountains, New York) whereas the Canadaway, Conneaut and Conewango are there totally lacking. At west, the exceptional thinning of the beds (to a twentieth or less), and their submergence under lake Erie, remove from view the Genesee, Naples and Chemung groups, leaving from Dunkirk, New York, westward into Ohio only those three groups visible that are absent at the east. But the facial changes have been such that these three were long identified with the lower (here concealed) groups, the Canadaway as "Portage," the Conneaut as "Chemung" and the Venango as (marine) "Catskill."

These relations of the several facies are brought out in the chart by differen styles of lettering, the black shales of "Genesee" facies by heavy-faced and the "Portage" (or Naples, or cardioconch) facies by thin-faced slanting letters (italics), the "Chemung" (or brachiopod) facies by plain upright, the "Catskill" red-beds facies by interrupted and the "Pocono" ("white" sandstone) facies by dotted upright (roman) letters. Merely casual inspection of the chart will therefore show how, in the middle column (which is the only complete one), the black shales of the true Genesee are at the bottom, overlain by the (type) 'Portage" beds from (7) Cashaqua to (16) Hanover, immediately over which one enter the "Chemung" facies and comes finally at top into red continental deposits of the "Catskill" phase. But one can start equally well at west in the black facies of the (8-9) Attica shale and pass horizontally eastward through contemporaneous facies of the same deposits, in the same order, into the true Catskill red, or from (15) Pipe Creek blacks into finally the type Pocono, once believed to be Mississippian.

Considering the major breaks in the stratic and faunal records of this Upper Devonian succession, the Chemung is now seen to fall into the Senecan epoch, which will include the Genesee, Naples and Chemung groups, or whole of the familiar "Portage." The Canadaway and Conneaut groups make up the Chautauquan, covering most of Chautauqua county, New York, in which the true Chemung is nearly absent, while the Conewangan comprises the former Bradfordian except such summit members (Knapp, Kushequa) as are now classed as Mississipian by Caster. Complete faunal analyses of these six

Upper Devonian groups will soon be published elsewhere, as well as of the seventh, or Cussewago, which in our contention is also Devonian.[2]

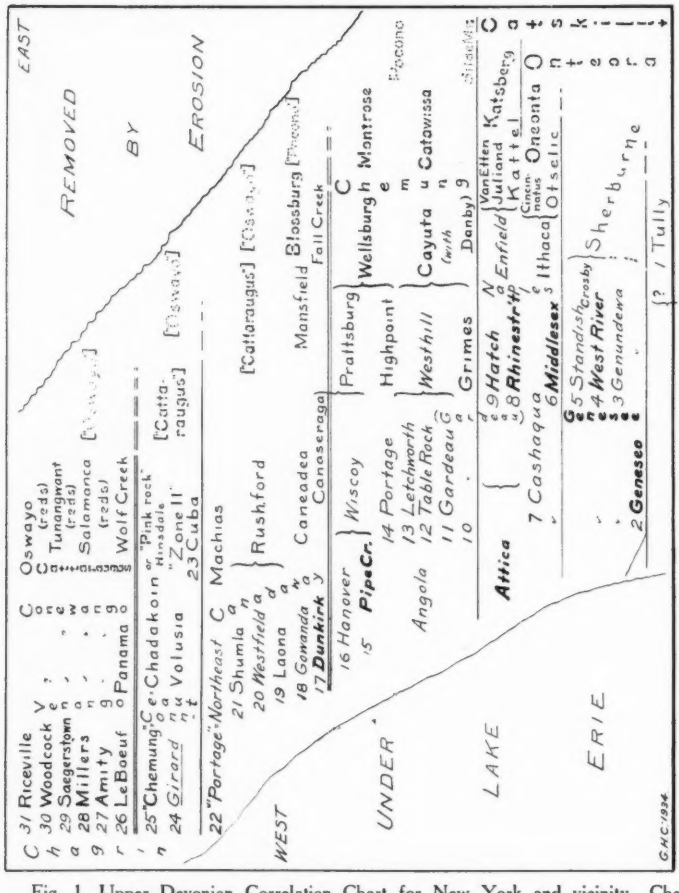


Fig. 1. Upper Devonian Correlation Chart for New York and vicinity. Check marks indicate presence of strata named in an adjoining column.

[2] Recently a doubt has arisen as to the correctness of the correlations above the (17) Dunkirk beds from Lake Erie to the Genesee river. It is possible that the (23) Cuba sandstone of the latter section belongs as low as the (21) Shumla sandstone on Lake Erie, which will necessitate changes in this numbering and a realinement of these higher formations at the west.

CATSKILL, N. Y.

THE ABERRANT SECONDARY SEX CHARACTERS OF THE CRAYFISHES OF THE GENUS CAMBARUS

C. L. TURNER

Introduction

This paper is written for the purpose of summarizing the results obtained from a fifteen year study of the secondary sex characters of some species of the crayfishes belonging to the genus Cambarus. Very brief accounts, some by the writer, have been published from time to time as new peculiarities have been found but it has not been possible to keep descriptions abreast of the finding of new specimens or new types of aberrant conditions. Nowhere has there been an attempt to bring together all this information so that it might be considered in its entirety and any likely conclusions drawn from it. Such an attempt is made in this paper.

Between 1920 and 1924 the writer made an intensive survey of the streams and lakes of southern Wisconsin and northern Illinois. Between fifty and sixty thousand specimens were examined. Later, collections were examined at Ohio State University, Wisconsin University, the Museum of Zoology at the University of Michigan and the Museum of Natural History of the University of Illinois. A collection was made by the Ohio Fish and Game Commission by a survey party of which the writer was a member and the opportunity was utilized to search for specimens with aberrant secondary sex characters. During the summers of 1925 and 1926 the writer was engaged as Biologist for the Wisconsin State Board of Health and surveys were made of the streams of northern and northeastern Wisconsin. The collections made during the course of this work were examined and yielded some new localities and new types of aberrancies. The writer is indebted to many individuals for smaller collections. Among them are Dr. David Thompson, of the Illinois Natural History Laboratory; Dr. E. P. Creaser, of the Museum of Zoology, University of Michigan; Professor R. C. Osburn, of Ohio State University; Dr. Ed. Wicliffe, of the Ohio Fish and Game Commission and Professor Paul Visscher of Western Reserve University. Collections made by supply companies especially in Louisiana and near Green Bay, Wisconsin have added considerable data. Finally, the writer collected in the field and examined about six hundred specimens at Cordoba, Mexico, Mexico City and at Lake Chapala near Ocotlan. Altogether, over 150,000 specimens have been examined for aberrant conditions of the secondary sex characters and the proportionate number of specimens with aberrant characters has been found to be surprisingly high.

Included in this report are the cases reported in the publications of Faxon, Hay, Ortmann and others. Although the attempt has been made to bring together the records of all such cases it is probable that some records have appeared in print which have been overlooked.

The collection made by the writer and some of the specimens donated by individuals have been deposited in the Smithsonian Institution.

Normal Secondary Sex Characters

Sexual dimorphism is apparent externally in various characters which are associated directly with the process of reproduction and in other features such as width of abdomen, dimensions of claws, etc., which are not. Only those characters are considered here which are directly concerned with reproduction.

In the male the following characters of this type are found: a pair of copulatory hooks on the third segment of the third walking legs; a pair of pores on the basal segment of the fifth walking legs, representing the openings of the genital ducts; a pair of modified swimmerets on the anterior abdominal segment, used for transferring the sperm from the openings of the genital ducts to the annulus ventralis of the female; a second pair of modified abdominal appendages located on the second abdominal segment, also used in the transfer of sperm to the annulus ventralis of the female.

In the female the structures visible externally which are used in reproduction are: (1) a pair of oviducal pores located on the basal segment of the third walking leg; (2) an oval annulus ventralis or sperm receptacle attached to the ventral side of the thorax between the fourth and fifth walking legs.

Classification and occurrence of aberrant types of secondary sex characters

Variations from normal secondary sex characters may be classified into three groups, (1) those cases in which characters normal for one sex are found to occur upon the other sex, (2) those cases in which characters normal to one sex are found wanting or supernumerary in that sex, (3) a small miscellaneous group.

Individuals in the first class are frequently referred to as "intersexes" or "hermaphrodites." The identification of an individual as hermaphroditic should always rest upon the finding of an ovo-testis or at least the finding of some tissue of the gonad of the opposite sex. Such cases are extremely rare. In the opinion of the writer the occurrence of a secondary sex character normal to one sex upon an individual of the other sex does not justify the conclusion that the individual is intermediate as far as sex is concerned. Most of the females, at least, which have had a full complement of male characters have been normally functioning specimens, maturing their eggs, copulating and later carrying embryos in the normal manner.

A few specimens have been found which had supernumerary characters of the same sex in addition to one or more characters of the opposite sex. The significance of the occurrence of supernumerary sex characters of the same sex will be discussed later in the paper.

Hermaphroditism, in the two or three cases listed is teratological in character, is associated with unusual combinations of secondary sex characters and is given a separate classification.

1. *Cases in which individuals of one sex have one or more additional characters of the opposite sex.*

a. *Males with oviducal pores.*

Wherever possible these males were dissected and in every case were found to have the appearance of normal males with no oviduct attached to the oviducal pore. The occurrence of the pore was bilateral in all but two cases. The pore always occurred at the base of the third walking leg in the position normal for this structure in the female. Following is the list of records for such cases:

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. *affinis*	Lake at East Hampton, Conn.		Atkins (described by Andrews)	1	
C. *diogenes*	Coldwater Crk., St. Jos., Mich.	April 1909	Conover	1	
C. *diogenes*	Urbana, Illinois		Van Cleave	1	
C. *obscurus*	Meander Crk., Pymatuning R. and No. 3 Creek, Girard, Ohio	August 1926	Ohio Fish & Game Com.	7	5+
C. *propinquus*	Turtle Creek, Rock Co., Wis.	July 1923	Writer	1	
C. *propinquus*	Turtle Creek, Rock Co., Wis.	August 1924	Writer	1	
C. *virilis*	Tributary of Sugar Creek, So. Wisconsin	August 1922	Writer	1	
C. *virilis*	Tributary of Rock River near Beloit, Wisconsin	July 1924	Writer	1	

b. *Females with copulatory hooks.*

In every specimen described or examined the copulatory hooks occurred on the third segment of the third walking legs, the normal position for the male. The degree of development varied from slight to complete and in cases where they were well developed the hooks were identical in character with those of the male. In a few cases the hook was developed on one side only. All those that were dissected had normal ovaries and oviducts.

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. bartoni	Holliday's Cove, Hancock Co., West Virginia	May 31, 1905	Ortmann, Car. Mus. Cat. 74491	1	
C. obscurus	Creek in Trumbull Co., O.	August 1926	Visscher	2	
C. obscurus	Pymatuning River, Trumbull Co., O.	August 1926	Ohio Fish & Game Com.	2	2
C. propinquus	So. Kinni Kinnick Creek, Winnebago Co., Ill.	July 1923	Writer	7	7
C. propinquus	Turtle Creek, Rock Co., Ill.	July 1923	Writer	9	
C. propinquus	Pike River, Racine Co., Wis.	July 1923	Writer	7	12+
C. propinquus	Root River, Racine Co., Wis.	July 1923	Writer	3	3—
C. propinquus	Nenomenee River, Milwaukee to Menomenee Falls, Wis.	July 1923	Writer	123	32—
C. propinquus	Milwaukee River, just north of Milwaukee, Wis.	July 1923	Writer	1	
C. propinquus	Cedar Creek at Hamilton, Wis.	July 1923	Writer	11	5+
C. propinquus	Fox river, near Waukesha, Wis.	July 1923	Writer	3	3+
C. propinquus	Coon Creek, Rock Co., Wis.	July 1923	Writer	2	12
C. propinquus	Tributary of Wisconsin River near Middleton, Wis.	July 1923	Writer	11	20
C. propinquus	Branch of Pecatonica River at Monro, Wis.	July 1923	Writer	1	
C. propinquus	Muskego Lake, Wis.	July 1924	Writer	2	
C. propinquus	Branch of Root River, Racine Co., Wis.	July 1923	Writer	1	
C. propinquus	Cedar Creek, at Horns Corner, Wisconsin	July 1923	Writer	3	
C. propinquus	Cedar Creek, at Jackson, Wis.	July 1923	Writer	2	32+
C. propinquus	Stream at Port Washington, Wisconsin	July 1923	Writer	1	
C. propinquus	Milwaukee River, at Waubackee, Wis.	August 1923	Writer	7	13
C. propinquus	North Fork of Milwaukee River at Filmore, Wis.	August 1923	Writer	6	5+
C. propinquus	Milwaukee River, at Newburg, Wisconsin	August 1923	Writer	8	14
C. propinquus	Fox River, at Waukesha, Wis.	July 1923	Writer	1	
C. propinquus	Rock River, near Rockford, Ill.	August 1926	Thompson	4	11
C. propinquus	Cedar Creek, near Hamilton, Wisconsin	July 1923	Writer	4	10+
C. propinquus	Milwaukee River, at Grafton, Wisconsin	July 1923	Writer	2	
C. propinquus	Milwaukee River at Thiensville, Wisconsin	July 1923	Writer	16	16
C. propinquus	Milwaukee River at Saukville, Wisconsin	July 1923	Writer	2	
C. propinquus	Milwaukee River at junction with North Fork	July 1923	Writer	2	
C. propinquus	Bass Creek, near Afton, Rock County, Wisconsin.	June 1923	Writer	2	
C. propinquus	Blasing, Michigan	Aug. 13, 1915	U. of Mich. Mus. Zool. No. 93620	1	

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. propinquus	KinniKinnick Creek, Winnebago Co., Wisconsin.	June 1924	Writer	3	
C. virilis	Delavan Lake, Walworth Co., Wisconsin.	1923, '24, '26	Writer	1140	87.7
C. virilis	Fox River, above Green Bay, Wisconsin.	August 1923	Supply Co.	2	
C. virilis	Tributary of Sugar River, Green Co., Wis.	August 1923	Writer	2	
C. virilis	Pond at Beloit, Wis.	June 1922	Writer	1	
C. virilis	Turtle Creek, Rock Co., Wis.	June 1922	Writer	2	
C. virilis	Lake Geneva, Williams Bay, Wisconsin	June 1923	Writer	1	
C. virilis	Root River, Racine Co., Wis.	July 1923	Writer	1	
C. virilis	Menomenee River, Milwaukee, to Menomenee Falls, Wis.	July 1923	Writer	1	
C. virilis	Fox River, near Waukesha, Wisconsin.	July 1923	Writer	1	10
C. virilis	Middleton, Wisconsin.	July 1923	Writer	1	
C. virilis	Coon Creek, Rock Co., Wis.	July 1923	Writer	1	
C. virilis	Branch of Root River, Racine Co., Wisconsin.	July 1923	Writer	2	9+
C. virilis	Milwaukee River, at Newbury, Wisconsin.	August 1923	Writer	1	
C. virilis	Wolfe River, at Keshena Falls, Wisconsin.	August 1926	Writer	2	16+
C. virilis	Fox River, between Green Bay and De Pere, Wisconsin.	July 1926	Writer	240	8
C. virilis	Wis. R., between Rhinelander and Wisconsin Rapids, Wis.	July 1926	Writer	11	2.5
C. virilis	E. River, near Green Bay, Wis.	July 1926	Writer	128	6+
C. virilis	Rock River, near Rockford, Ill.	August 1926	Thompson	11	11
C. virilis	Robinson Creek, Roscommon, Michigan.	August 1924	Hankinson	4	
C. virilis	Muskego Lake, Wisconsin	July 1924	Writer	3	4
C. virilis	Fox River, Wisconsin	August 1927	Supply Co.	1	
C. rusticus	Bluffton, Indiana	April 5, 1909	Williamson	1	

c. *Females with first abdominal appendages of male*

Seldom is there a case in which the development of the first abdominal appendage is equal to that of the normal male. In the normal female the first abdominal appendages are rudimentary and any increase in size becomes noticeable. However, only those cases are included here which have considerable development and in which there is some fusion and twisting of the rami. In two of the cases the development was unilateral.

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. diogenes	North Judson, Indiana		Sphung (H. J. Van Cleave's collection)	1	
C. diogenes	Stream near Urbana, Illinois		Van Cleave	1	
C. diogenes	New Orleans, Louisiana		Faxon (Mus. Com. Zool. 242)	1	
C. gracilis	Normal, Illinois	1882	Forbes	1	
C. obscurus	Creek in Trumbull Co., Ohio	August 1926	Visscher	1	
C. propinquus	Embarass River, Illinois	1911	Ill. Nat. Hist. Mus. 45301	1	
C. propinquus			Faxon (Mus. Com. Zool. 3432)	1	
C. propinquus	Huron R., near Dexter, Mich.	Sept. 24, 1931	Creaser	1	
C. propinquus sanborni			Faxon (Mus. Com. Zool. 3588)	1	
C. rusticus	Wabash River, at Bluffton, Ind.	June 1, 1905	Williamson (described by Ortmann) Carnegie Mus. Cat. 74.578	1	

d. *Females with first and second abdominal appendages of male.*

In the two specimens listed, the first and second abdominal appendages were completely developed and hardly distinguishable from those of a normal male. One of the two was carrying embryos.

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. propinquus	Turtle Creek, at Beloit, Wis.	April, 1922	Writer	2	

e. *Females with copulatory hooks and in addition, first abdominal appendages of male.*

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. virilis	Lake Delavan, Wisconsin	June, 1923	Writer	1	

f. *Females with copulatory hooks and in addition, first and second abdominal appendages of male.*

Specimens of this type have an almost complete equipment of both male and female secondary sex characters. All ten taken by the writer had normal ovaries and oviducts and three taken in April were carrying embryos.

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. obscurus	Ohio River, at Neville Island	May 14, 1899	Atkinson (described by Ortmann)	1	
C. propinquus	Turtle Creek, at Beloit, Wis.	April, 1922	Writer	6	2.5
C. propinquus	Turtle Creek, at Beloit, Wis.	July, 1923	Writer	3	
C. propinquus	Turtle Creek, at Beloit, Wis.	July 5, 1924	Writer	1	
C. spinosus	Clinch River, Tenn.	Oct. 12, 1893	Everman (described by Hay) U. S. Mus. 20,835	2	

2. *Cases in which individuals have supernumerary secondary sex characters or in which characters are lacking.*

a. *Males with copulatory hooks on second walking legs in addition to those on the third walking legs.*

This condition, while aberrant for the species listed here, is normal for all species of the sub-genus Cambarellus.

In many cases the hooks on the second walking legs were as well developed as those on the third legs. It was quite common, however, to find small or partially developed hooks on the second walking legs. In all cases hooks are present upon the second legs only when also present upon the third legs.

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. obscurus	Pymatuning R., Girard, Ohio	1926	Ohio Fish & Game Com.	3	
C. obscurus	E. Mahoning Creek, Mahoning Co., Ohio		Ohio St. U. Museum	2	
C. propinquus	Ashtabula Co., Ohio	1899	Ohio St. U. Museum	1	
C. propinquus	Birmingham, Michigan	July 1905	Field	2	
C. propinquus	Walnut L., Oakland Co., Mich.	Nov. 1905	Adams	1	

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. *propinquus*	White Pigeon, Michigan	April 1909	U. of Mich. Mus. Zool.	4	
C. *propinquus*	Geddes Dam, Washtenaw Co., Michigan	April 1909	U. of Mich. Mus. Zool.	1	
C. *propinquus*	Swan Creek, Newport, Mich.	April 1907	Hankinson	1	
C. *propinquus*	Otter Creek, LaSalle, Mich.	August 1917	U. of Mich. Mus. Zool.	1	
C. *propinquus*	River Raisin, Monroe, Mich.	1920	Hubbs	1	
C. *propinquus*	Turtle Creek, Rock Co., Wis.	1922	Writer	2	
C. *propinquus*	Turtle Creek, Rock Co., Wis.	1923	Writer	3	
C. *propinquus*	Kinnikinnick Crk., Winnebago Co., Illinois	1923	Writer	3	
C. *propinquus*	Carvers Rock Creek, Rock Co., Wisconsin	July 1923	Writer	2	
C. *propinquus*	Pike Co., Racine Co., Wis.	July 1923	Writer	15	
C. *propinquus*	Menomenee River, Milwaukee, Wisconsin.	July 1923	Writer	11	8+
C. *propinquus*	Cedar Crk., at Hamilton, Wis.	July 1923	Writer	2	
C. *propinquus*	Fox River, at Waukesha, Wis.	July 1923	Writer	2	
C. *propinquus*	Sugar River, Green Co., Wis.	July 1923	Writer	1	
C. *propinquus*	Stream at Port Wash'ton, Wis.	August 1923	Writer	6	4—
C. *propinquus*	Milwaukee River, at Waubackee, Wisconsin	August 1923	Writer	3	
C. *propinquus*	Milwaukee R., at Brown Creek, Wisconsin	August 1923	Writer	2	
C. *propinquus*	So. Kinnikinnick Creek, Winnebago Co., Illinois	August 1923	Writer	8	3—
C. *propinquus*	Rock River, near Rockford, Ill.	August 1926	Thompson	2	
C. *propinquus*	Douglas Lake, Michigan		U. of Mich. Mus. Zool.	9	12—
C. *propinquus*	Stream at Chelsea, Michigan		Hagle	1	
C. *propinquus*	Stream near Urbana, Illinois		VanCleave	1	
C. *propinquus*	North Fork of Milwaukee R., at Filmore, Wis.	August 1924	Writer	3	3
C. *propinquus sanborni*	Sandusky Bay, Sandusky, Ohio	October 1905	U. of Mich. Coll. Mosley, 32858	1	
C. *virilis*	Marquette, Michigan	June 1905	Reed	1	
C. *virilis*	Bear L., Houghton Co., Mich.	August 1905	U. of Mich. Mus. Zool.	1	
C. *virilis*	Douglas Lake, Michigan	April 1909	U. of Mich. Mus. Zool.	1	
C. *virilis*	Clinger Lake, Michigan	April 1909	U. of Mich. Mus. Zool.	2	
C. *virilis*	Pine River, Marquette, Mich.	June 1909	U. of Mich. Mus. Zool.	1	
C. *virilis*	Sturgeon River, Dickinson Co., Michigan	August 1909	Ruthven and Baker	2	
C. *virilis*	Lake Superior, at White Fish Point	1914	U. of Mich. Mus. Zool.	1	
C. *virilis*	Tributary Rock R., Rock Co., Wisconsin	1921	Writer	2	

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. virilis	Houghton Lake, Roscommon Co., Michigan	August 1922	Creaser	1	
C. virilis	Fox River, Brown Co., Wis.	August 1922	Supply Co.	18	3.5
C. virilis	Coon Creek, Rock Co., Wis.	July 1923	Writer	1	
C. virilis	Root River, Racine Co., Wis.	July 1923	Writer	5	17+
C. virilis	Browns Lake, Racine Co., Wis.	July 1923	Writer	2	
C. virilis	Menomenee River, above Milwaukee, Wisconsin.	July 1923	Writer	2	
C. virilis	Menomenee River, near Menomenee Falls, Wis.	July 1923	Writer	4	
C. virilis	Muskego, Lake, Waukesha Co., Wisconsin.	July 1923	Writer	1	
C. virilis	Stream at Port Wash., Wis.	August 1923	Writer	2	
C. virilis	Milwaukee River, at Filmore, Wisconsin	August 1923	Writer	1	
C. virilis	Houghton Lake, at Roscommon, Mich.	1925	Hankinson	1	
C. virilis	Wisconsin River, at Wisconsin Rapids, Wisconsin.	July 1926	Writer	42	19—
C. virilis	Fox R., near Green Bay, Wis.	August 1926	Writer	460	17—
C. virilis	E. River, near Green Bay, Wis.	August 1926	Writer	262	14—
C. virilis	Rock River, near Rockford, Ill.	August 1926	Thompson	12	11—
C. virilis	L. Huron, at Port Austin, Mich.		U. of Mich. Mus. Zool.	1	
C. virilis	Stream near Urbana, Ill.		Van Cleave	1	
C. virilis	Stream near Urbana, Ill.		Ill.Nat.Hist. Mus. 151a 24996	3	
C. virilis	Stream near Urbana, Ill.		Ill.Nat.Hist. Mus. 151a 28194	1	
C. virilis	Milwaukee River, at Newbury, Wisconsin	August 1924	Writer	1	

b. *Males with copulatory hooks on fourth walking legs in addition to those on the third walking legs.*

In most cases the hooks on the fourth legs were as well developed as the normal ones on the third legs. Hooks occurred on the fourth legs always in connection with the occurrence of hooks upon the third legs.

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. propinquus			Collector Ill.Nat Hist. Mus. 24966	2	
C. propinquus	Turtle Creek, Rock Co., Wis.	June, 1922	Writer	3	
C. propinquus	Carvers Rock Creek, Rock Co., Wisconsin	June, 1923	Writer	2	
C. propinquus	Lake Delavan, Walworth Co., Wisconsin	June 30, 1923	Writer	1	
C. propinquus	So. Kinnikinnick Creek, Winnebago Co., Illinois	July 26, 1923	Writer	3	3
C. propinquus	Pike River, Racine Co., Wis.	July 9, 1924	Writer	6	17
C. propinquus	Fox River, at Waukesha, Wis.	July 18, 1924	Writer	1	

c. *Males with copulatory hooks on the second and fourth walking legs in addition to those on the third walking legs.*

This rare condition, not a normal one in any crayfish, was found in only two localities. It is significant that three specimens were found in one of these localities.

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. virilis	Cheyenne, Michigan		U. of Mich. Mus. Zool. 9942	1	
C. propinquus	Pike River, Racine, Wis.	July, 1923	Writer	3	1.25

d. *Males with third abdominal appendages modified like second abdominal appendages.*

It is assumed that the peculiar structure in the second abdominal appendages is associated functionally with copulation. A modification in the third pair of appendages causes this pair of swimmerets to resemble the second pair. The modification shows various degrees of development from very slight to a modification almost completely like that in the second pair. It is not likely that there is any functional significance in this modification.

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. propinquus	Castalia Creek, Castalia, Ohio	July 7, 1929	Wicliffe	1	
C. virilis	Stream near Urbana, Illinois		VanCleave	1	
C. virilis	Fox R., near Green Bay, Wis.	July 1927	Supply Co.	46	15
C. virilis	Indiana	1903	Moenkhaus	1	
C. virilis	Menomenee River, near Menomenee Falls, Wis.	July 1923	Writer	1	

e. *Males with third abdominal appendages modified like second abdominal appendages and also copulatory hooks on the second walking legs in addition to those on the third walking legs.*

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. propinquus	Menomenee R., near Menomenee Falls, Wisconsin	July, 1923	Writer	1	

f. *Females with supernumerary oviducal pores on second thoracic legs in addition to those on the third legs.*

In both species in which this peculiarity has been found, supernumerary oviducal pores on the fourth legs have been sought but none have ever been found.

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. propinquus	Carvers Rock Creek, Rock Co., Wisconsin	July 16, 1923	Writer	2	4
C. propinquus	Kinnikinnick Creek, Winnebago County, Illinois	June 30, 1924	Writer	1	
C. propinquus	White R., Walworth Co., Wis.	July 2, 1924	Writer	1	6.6
C. propinquus	Pike R., Racine Co., Wis.	July 9, 1924	Writer	1	
C. propinquus	Turtle Creek, Rock Co., Wis.	July 3, 1924	Writer	1	
C. propinquus	Flint Creek, Flint, Mich.	1909	Kaufman	1	
C. propinquus	School Section Creek, Graylings, Mich.	1924	Hankinson & Laughlin	1	
C. virilis	Wis. R., at Wis. Rapids, Wis.	July, 1926	Writer	7	2.2+
C. virilis	Tributary of Wis. R., near Middleton, Wis.	July 22, 1924	Writer	1	
C. virilis	Outlet of Muskego Lake, Wis.	July 11, 1924	Writer	1	4

f. *Females lacking an oviducal pore on one side.*

Species	Locality	Date	Collector	No. of specimens	Proportion of total in %
C. propinquus	Turtle Creek, Rock Co., Wis.	July 5, 1924	Writer	1	
C. virilis	Browns Lake, Michigan	Apr. 14, 1909	Baker	1	
C. virilis	Rock R., near Rockford, Ill.	August 1926	Thompson	1	
C. virilis	Browns Lake, Michigan	July 2, 1905	Baker	1	

g. *Specimens with annulus ventralis not normal.*

Case 1. Two specimens of *C. spinosus* collected from Clinch River, Tenn., by Everman on Oct. 12, 1893; described by Hay; U. S. Nat. Mus. No. 20835. Annulus ventralis a little less developed than normal, otherwise a normal female with following male characters in addition: first and second abdominal appendages like male but a little undeveloped, unperforated genital papilla at base of fifth legs. The internal organs were like those of a normal female.

Case 2. Specimen of *C. bartoni* collected from Fern Hollow, Pittsburgh, Pa., on November 22, 1905 by Ortmann. Car. Mus. Cat. No. 74,681.

Annulus ventralis of the juvenile type; no copulatory hooks nor oviducal pores on the third legs; genital openings at the base of fifth legs; first abdominal appendages like those of male.

Case 3. Specimen of *C. propinquus* collected at Sandusky, Ohio, by Hay. Annulus ventralis lower than usual. Marked lack of symmetry on the two sides. Left side: copulatory hook on third leg; genital duct at base of fifth leg; first and second abdominal appendages imperfectly developed but male-like. Right side: oviducal pore on third leg; first abdominal appendage male-like but not fully developed.

Case 4. Specimen of *C. propinquus* collected September 24, 1931, from Huron River, near Dexter, Michigan, by Creaser. External structures: first and second abdominal appendages modified like male but slender, no hooks on third walking legs; an imperfect oviducal pore on third leg on one side; annulus ventralis partially developed but with specific features of the species; normal openings for sperm ducts at base of fifth walking legs. Internal structures: normal testis and sperm ducts; four small isolated ovarian masses above and at side of testis.

Case 5. Specimen of *C. propinquus:* same locality, date and collector as case 4. External structures like those of case 4, except that the annulus ventralis was not so well developed; internal structures like those of case 4, except that the ovarian masses were more extensive.

Case 6. Specimen of *C. obscurus* collected from Allegheny River at Sandy Creek, Pa., on November 19, 1904, by Ortman. Car. Mus. Cat. No. 74, 479.

Annulus ventralis with outlines visible but indistinct; no copulatory hooks on third legs; genital openings at the base of fifth legs; first and second abdominal appendages male-like.

3. Miscellaneous types.

A. *Specimens with supernumerary characters of the same sex in addition to characters of the opposite sex.*

Case 1. Male of *C. virilis* with supernumerary copulatory hooks on the second walking legs in addition to those on the third legs; also an oviducal pore on one of third walking legs. Collected in July, 1926, from Wisconsin River, at Wisconsin Rapids, Wisconsin, by writer.

Case 2. Female of *C. propinquus;* oviducal pore on one of fourth walking legs in addition to those on the third walking legs; rudimentary male genital pores at the base of fifth walking legs; first and second abdominal appendages modified like those of male; collected in Turtle Creek, at Beloit, Wisconsin, April, 1923, by writer.

B. *Females utilizing male genital pores on fifth walking legs as oviducal openings.*

Case 1. *C. propinquus sanborni* collected by Faxon. Collection of Mus. Comp. Zool., No. 3350.

Case 2. *C. immunis* collected by writer from Root River, near Racine, Wisconsin, July 10, 1924.

C. *Specimens with functional or non-functional hermaphroditism and aberrant secondary sex characters.*

Case 1. Specimen of *C. affinis* from Potomac River, near Washington; collected by W. P. Hay; Externally like normal male except that oviducal openings were present on third walking legs and openings of sperm ducts at base of fifth walking legs were rudimentary; internally like normal female except that small testis is present on right side and a small sperm duct leading to rudimentary opening at base of fifth walking leg.

See also above cases 4 and 5 under "annulus ventralis not normal."

Discussion

1. Copulatory Hooks

In looking over the long list of cases in which copulatory hooks occur on the second or fourth legs of males in addition to those occurring with absolute constancy on the third legs, one is impressed with the fact that this peculiarity is not a mere accidental phenomenon but rather that a definite tendency toward additional hooks is indicated. The impression is given additional weight when it is noted that in some localities the peculiarity is present in a reasonably large proportion of the whole male population. The list of cases in which females also bear a copulatory hook upon the third leg is equally impressive especially when it is noted that in one locality 32 per cent of all the females of one species and in another locality 87 percent of all the females of another species are so equipped.

The full significance of these supernumerary hooks can be appreciated only when one reviews the phylogeny of the sub-genera of the genus and the history of the origin of supernumerary hooks during the evolution of the sub-genera. Ortmann (1905) presents evidence for the fact that the most ancient sub-division existed in South Central Mexico before the Cetaceous period. This ancient sub-genus already had the copulatory hooks fixed on the third legs of the males. This old sub-genus Cambarus gave rise to a second sub-genus, Cambarellus, while still in Central Mexico. One of the distinctive features of this second sub-genus was the development of a second pair of hooks, the additional ones being on the second legs. *C. montezumae* represents this type. Apparently this new arrangement of hooks (on second and

third legs) arose as a mutation from the older stock with hooks on the third legs only. Some members of the old stock still retained the old arrangement of hooks on the third legs only and a part of this stock migrated northward over the high plains of Texas into Kansas where it is still found. Then an eastward migration took place, one sub-division turning northward to reach southern Wisconsin. *C. gracilis* with hooks only on the third legs represents this sub-division today. Another sub-division moved southeastward and in the region from eastern Missouri to northern Alabama gave rise to three of the modern sub-genera. (1) Cambarus represented by *C. clarkii* and others remained in the south, *C. blandingii* and *C. blandingii acutus* migrated northward. This sub-genus, as it was formed, mutated in the direction of the formation of an additional pair of hooks but in this instance the extra hooks were located upon the fourth legs. Hooks upon the third and fourth legs of males are now diagnostic for this sub-genus Cambarus. (2) Faxonius arose from the old Cambarus stock before the mutation occurred and so retained the hook only upon the third leg. Later *C. (Faxonius) pellucidus*, a cave species from Kentucky, produced a mutation parallel to that of the sub-genus Cambarus and hooks are now found in this species upon the third and fourth legs of males. (3) Bartonius also arose from the old Cambarus stock before it mutated and still retains the old condition of hooks only upon the third legs.

If the occurrence of supernumerary hooks, as shown in the list in this paper, is viewed in the light of these former mutations it becomes evident that the sub-genus Faxonius is still producing mutations parallel to those which it has produced in the past. Mutations with hooks upon the second and third legs are now appearing in both *C. (Faxonius) virilis* and *C. (Faxonius) propinquus* and indicate an event parallel to that which produced the sub-genus Cambarellus. This is especially marked in *C. virilis*. Mutations with hooks upon third and fourth legs are occurring in *C. propinquus* and are parallel to the change that took place when the modern sub-genus Cambarus arose from the older Cambarus stock and again, when, within the sub-genus Faxonius, *C. pellucidus* mutated in the direction of developing additional hooks upon the fourth legs. An interesting combination of two mutations is represented apparently in Pike River, near Racine, Wisconsin. Three speciments were found in which hooks were present on second, third and fourth legs. In this locality there is a considerable abundance of what appears to be two separate stocks, one with hooks upon the second and third legs, and the other with hooks upon the third and fourth legs. A crossing of these two stocks apparently gave rise to the stock having hooks on the second, third and fourth legs.

There is no precedent in the evolution of the genus for a large scale mutation in the direction of the appearance of a copulatory hook on the third leg of the female. However, varieties of this type are now being established in *C. propinquus* and especially in *C. virilis*. In Delavan Lake less than fifteen per cent of the females of *C. virilis* are "normal" in having no hooks upon the third legs while more than eighty-five per cent are "abnormal" in having these hooks. There seems to be no relation between these hooks and sex in the race established in Lake Delavan. The females reproduce normally and examina-

tion by dissecting and sectioning have not so far yielded any specimens with testicular tissue. It is an interesting fact that the hooks in the females are identical in both position and character with those of the male and it is hardly possible to escape the conclusion that the females bear the same genetical determiner or determiners for this character as the males. This raises the further question as to whether these females are unique in possessing this determiner or whether all females do not bear a determiner for hooks on the third legs and at the same time an inhibitor for its development. If an inhibitor is present it is apparently a genetical one and not a hormonal one produced in the ovary. In this peculiar stock either a genetical inhibitor for the development of the hooks has been removed or the determiner for the hook has somehow been shifted from some male germ plasm to the germ plasm of the female and fixed there so that it now appears in both sexes.

2. Abdominal Appendages

Females with partially or fully developed first or second abdominal appendages occur in the three sub-genera Faxonius, Bartonius and Cambarus (one case in *Cambarus gracilis*). Male abdominal appendages in the female occur either separately or in combination with copulatory hooks on the third legs and, as already stated, copulatory hooks occur in many cases without the modified abdominal appendages. It is apparent, therefore, that each condition is a separate mutation. There are several instances in which only the first appendage is modified, a less number in which both first and second abdominal appendages are modified and none at all in which only the second is modified. In a very few instances only are both appendages as fully and specifically developed as in the normal male. Again when the question is raised as to the source of the mutation, two alternatives present themselves. (1) That in some manner a determiner has been transferred from the male to the female germ plasm or, (2) that females regularly carry the gene for these characters and that some genetic or hormonal inhibitor ordinarily prevents the gene from producing the character. Presumably the determiner for those two appendages in the male is compound or there are several genes operating together and when this complex is transferred to the female it is somtimes broken up and only a part of it transferred with the result that only one appendage is modified or both are imperfectly modified. Another possibility of interference with the full and specific development in the female of these two male appendages may be the determiners which already exists in the female for rudimentary first abdominal appendages.

The peculiarity in the male consisting of third abdominal appendages modified to resemble the second abdominal appendages in addition to the normal already modified first and second abdominal appendages is another mutation. Apparently it arises only rarely but it has become fairly well established in the Fox River near Green Bay, Wisconsin, in *C. virilis*. Forty-six specimens were taken in this one locality. It is distinct from the mutation in which accessory hooks are present. The peculiarity never occurs in the form

of an isolated modification in the third abdominal appendages but always as an addition to the secondary sexual characters already present. Sometimes the modification is slight but when fully developed the modification in the third abdominal appendages is identical with that in the second abdominal appendages. The determiner for this peculiarity should be considered perhaps as an extension or modification of the complex factor which is already present in every normal male and which governs the direction of development in the first and second abdominal appendages.

3. Oviducal Pores

Variations from the normal condition of the oviducal pores consist of, (1) supernumerary pores in the female, and, (2) the lack of one of the pair of oviducal pores, (3) the occurrence of pores on the third legs of males.

(1) The pore on the third leg is always present and when pores occur upon the second legs they are always in addition to those already formed upon the third leg. The supernumerary ones are not always well developed and in some instances no oviduct is attached to them. When fully developed they are precisely like those on the third legs. Presumably these additional pores are caused by a mutation in the one or more genes which govern the character of the oviducal pores, the location of these on the third leg and the confinement of them to the third legs. Specimens with supernumerary pores from Wisconsin Rapids in the Wisconsin River indicate that in this locality the variation is becoming fairly well established. The tendency for the development of supernumerary oviducal pores is found also in the genus Astacus. Benham (1891) reports several instances in *Astacus fluviatilis* in which bifurcated terminal ends of oviducal tubes are attached to both pairs of openings. It might be argued from this relationship that the pores act as inductors and control the direction of growth of the oviducts. In these cases the extra pore would effect the developing oviduct so as to cause the outgrowth of a branch which would finally become connected with it.

(2) The lack of an oviducal pore on one side is not taken as particularly significant. The condition probably represents an accidental interference of some kind during embryological development. It is instructive to note that in some cases a blind oviducal tube is present on the side on which the pore is lacking. This indicates that the developing tube does not exercise an organizing influence upon the integument and so produce a pore. Apparently the pore develops independently and this is borne out by the fact that no vestiges of oviducal tubes are found in connection with the well developed pores that sometimes occur in males.

(3) When oviducal pores occur at all in males it is always in the position normal in females. When they are well developed in males they are precisely like those of normal females. As stated before they are not functional and are not connected to any oviducal tube. They probably bear the same relation to males as copulatory hooks do to females. Unless one assumes again that males bear factors for potential pores exactly like those of the females and

located in the same position it is necessary to account for their origin in the males by assuming that the determiners for them have in some way become transferred from the female to the male germ plasm. The only locality in which any particular concentration of this type has appeared is the Pymatuning River at Girard, Ohio, where seven specimens, representing a little over five per cent of all the males taken, were found. The concentration is too great to be explained on a purely accidental basis. Apparently a strain is being established here.

4. Male Genital Pores

There is practically no variation in character and none in the position of the male genital pores. In the two cases in which tubes lead from ovaries to openings at the base of the fifth legs a number of tentative theories might be advanced to account for the condition. It is quite possible that the openings are dislocated oviducal pores in which case it would be logical to find them with oviducts attached and functioning as outlets for eggs in spite of the peculiarity of their location. Or, it is possible that sex reversal might have taken place after the secondary sex characters were established. With a replacement of testis by ovary the gametes which would pass through the tubes attached to the fifth legs would be ova instead of sperm. A subsequent modification of both tube and outlet pores would produce the condition as it was found in these two specimens.

5. Annulus ventralis

Only six cases have been reported in which the annulus ventralis is in any way abnormal and this number is too small upon which to base any important generalizations. The facts in these cases when combined with those concerning the occurrence of the annulus in instances which have other peculiar conditions of the secondary sex characters make it possible to generalize a little further. (1) The annulus ventralis has not been reported and probably does not occur in any completely normal male. (2) There is nothing antagonistic between the factors producing or controlling copulatory hooks and male-like abdominal appendages on the one hand and the factors producing or controlling the annulus on the other. Many cases are listed in which a normal annulus and normal copulatory hooks are present in the same specimen and a lesser number of cases in which first and second abdominal appendages occur in specimens which possess a normal functional annulus. (3) A partially developed annulus may occur in the presence of normal male gonads, sperm ducts and external genital pores. This is demonstrated in cases four and five. It might also apply in cases two and six but these were not dissected and the conditions of ovary and spermary are not known. (4) Complete lack of an annulus seems to be associated only with the complete absence of ovarian tissue in normal males. (5) Unusual conditions are present in the annulus only when associated with other peculiarities in the secondary sexual characters.

The fact that the annulus ventralis is lacking only when there is a complete absence of ovarian tissue naturally leads to an inquiry of the nature of

the association. A hormonal relationship may be suggested as in birds and mammals where factors are carried for most of the secondary sex characters by all individuals but only those are completely developed in one sex which receive the appropriate hormonal stimulus. This would assume a genetic factor in the first place for the annulus ventralis in all specimens which eventually show it. In case four and five where the annulus is partially developed the animals seem to be functional males. In the case of these two it would be necessary to assume that some males also carry a determiner for the annulus or that these two were originally females and had undergone sex reversal. In the single specimen listed under functional or non-functional hermaphroditism we have a specimen without an annulus but with a well developed ovary. Possibly this specimen was originally a male and so did not bear a determiner for the annulus.

The question of the relationship of the annulus to sex will be further considered under the following topic.

Sex in relation to secondary sex characters

Among the Decapods are some forms which are regularly hermaphroditic. Calocaris and Gebia (Rünnstrom, 1926) have an ovo-testis which functions for a part of the season as a producer of male gametes and part of the time as a producer of eggs. Oviducts extend from the gonad to external pores at the bases of the third legs and sperm ducts from the gonad to the male genital pores on the fifth legs in each specimen. The South American crayfish Parastacus also has external pores on both the third and the fifth legs in each animal and it has been assumed that they were also hermaphroditic. Indeed, an hermaphroditic gland has been described by several authors. A collection of thirty-three specimens of *Parastacus hassleri* and of eleven specimens of *Parastacus saffordi* was loaned to the writer by the Smithsonian Institution and was examined. In none of these specimens was an hermaphroditic gland found. In the females a well developed oviduct was present and a rudimentary sperm duct. In the males the vas deferens was well developed and the oviducts rudimentary. The condition is suggestive of a former hermaphroditic condition which has now been given up as far as the gonads are concerned but with a retention to some extent of the ducts and external conditions that accompanied it.

With these cases in mind it might be postulated that an hermaphroditic condition once existed in Cambarus and that the occasional occurrence of oviducal pores in the males and of copulatory hooks and male-like first and second abdominal appendages in females represents an atavistic reappearance of these characters. An alternative point of view which is emphasized throughout this paper is that the determiners for these characters have in some manner become transferred and in some cases fixed in the germ plasm of the opposite sex.

The regular occurrence of a normal gonad with the secondary sex characters that usually accompany it does not mean necessarily that the gonad has an antagonistic action for the development of secondary sexual characters of the opposite sex. Copulatory hooks which usually accompany the spermary in the

male occur in eighty-seven percent of the females of *C. virilis* in Delavan Lake. Fully developed first and second abdominal appendages characteristic of the male also occur in some instances in females which reproduce normally. Oviducal pores usually accompanying the ovary in females are found in some instances in normally functioning males. In the case of the annulus ventralis it seems that some ovarian tissue is necessary for its development and that complete development only takes place in the absence of any testicular tissue.

Distribution of aberrant sexual characters in the different sub-genera

All the aberrant conditions of secondary sexual characters that have been reported are, with a single exception, found in the two sub-genera Faxonius and Bartonius. A single specimen of *Cambarus (Cambarus) gracilis* has a modified first abdominal appendage in the female. It is probable that because of their distribution larger numbers of specimens in the sub-genera Faxonius and Bartonius have come under observation. At the same time large numbers of *Cambarus (Cambarus) clarkii* have been used in laboratory studies and if unusual characters existed it is likely that they would have been noted. The writer examined a collection from a supply house of about six hundred specimens and not a single variation was found. On another occasion about three-hundred and sixty specimens of *Cambarus (Cambarus) blandingii* acutus were examined in the field in western Ohio and again no variations were found. A similar constancy seems to exist in the sub-genus Cambarellus which is confined to Mexico and Louisiana. The writer had the opportunity of collecting and examining several hundred specimens of this sub-genus from the lakes about Mexico City and from the Santiago River and Lake Chapala near Ocotlan. No variations in the secondary sexual characters were found in any of them.

The constancy in the sub-genera Cambarus and Cambarellus, at least as far as the copulatory hooks in the males are concerned, can be accounted for partly by the fact that the most common variations in other sub-genera occur in these characters. Cambarellus has already developed and fixed a condition which in Faxonius and Bartonius would be considered a variation, namely, an extra pair of hooks upon the second legs. In a similar manner the sub-genus Cambarus has developed and fixed an extra pair of hooks on the fourth legs. Since variation in the direction of loss of hooks already developed in the sub-genus does not occur in any sub-genus, there would be left only the possibility of hook development to a still greater degree. This hook development on second, third and fourth legs is extremely rare and has been found in the sub-genus Faxonius in only four of about 75,000 males examined.

REFERENCES

Since this paper is confined almost entirely to an account of secondary sexual characters in the genus Cambarus, the following list of references will contain principally papers and monographs referring to members of the genus. A few other papers are included to which references have been made in the discussion.

ANDREWS, E. A. 1909—A male crayfish with some female organs. Amer. Nat. **43**(512):461-471.

BENHAM, W. B. 1891—Notes on a couple of abnormalties. Ann. Mag. Nat. Hist., series 6, **7**:256.

FAXON, WALTER. 1885—A revision of the Astacidae. Mem. Mus. Comp. Zool. **10**:13.

———1898—Observations on the Astacidae in the United States. National Museum and the Museum of Comparative Zoology. Proc. U. S. Nat. Mus. **20**:683.

HAY, W. P. 1905—Instances of hermaphroditism in Crayfishes. Smithsonian Misc. Coll. **48**:222.

LONNBERG, EMAR. 1898—Some biological and anatomical facts concerning Parastacus. Zool. Anz. **21**:334-345.

MOENKHAUS, W. J. 1902—An extra pair of appendages modified for copulatory purposes in Cambarus virilis. Proc. Indiana Acad. Sci. **1902**.

ORTMANN, A. E. 1905—The mutual affinities of the species of the genus Cambarus and their dispersal over the United States. Proc. Amer. Philos. Soc. **44**:91.

———1906—The crawfishes of the state of Pennsylvania. Mem. Carnegie Mus. **2**(10):375-376, 387-388.

RUENNSTROM, SVEN. 1926—Beitrag zur Kenntnis einiger hermaphroditischen dekapoden Crustaceen. Bergen. Mus. Skr. **3**(2):1-116.

TURNER, C. L. 1924—Studies on the secondary sexual characters of crayfishes. I. Male secondary sexual characters in females of Cambarus propinquus. Biol. Bull. **46**(6):263-267.

———1925a—II. Females of Cambarus virilis with male secondary sexual characters. Biol. Bull. **48**(4):225-231.

———1925b—III. Males with supernumerary male secondary sexual characters in the subgenus Faxonius. Biol. Bull. **48**(4):232-235.

———1925c—IV. Male crayfishes with two sets of supernumerary male characters. Biol. Bull. **49**(5): 375-378.

———1925d—V. Male crayfishes with female characters. Biol. Bull. **49**(5):379-380.

———1928a—VI. A female of Cambarus immunis with oviducts attached to openings of sperm ducts. Biol. Bull. **55**(3):193-196.

———1928b.—VII. Regeneration of aberrant secondary sexual characters in crayfishes. Biol. Bull. **55**(3):197-201.

———1928c.—VIII. Modified third abdominal appendages in males of Cambarus virilis. Biol. Bull. **55**(4): 255-259.

———1929—IX. Females of Cambarus with aberrant female characters. Biol. Bull. **56**(1):1-7.

ZOOLOGICAL LABORATORY,
NORTHWESTERN UNIVERSITY,
EVANSTON, ILL.

THE ANATOMY OF THE FRESH WATER PROSOBRANCHIATE GASTROPOD, PLEUROCERA CANALICULATUM UNDULATUM (SAY)

SAMUEL R. MAGRUDER

Introduction

The *Pleuroceridae* have been known for more than a century, yet there has been but little work done on the anatomy or life history, and since representatives of this family make up an important part of the fresh water life of the Eastern half of the United States, a study of some phases of their biology seems particularly desirable (Magruder, 1934).

In the present anatomical investigation approximately 720 animals have been dissected. Serial sections of entire animals and of separate organs or regions have been made for the purpose of corroborating and extending the findings of gross dissections. The study of the microscopic anatomy has been limited largely to elucidating the general anatomy, and in describing structures that may have some taxonomic significance. The minute descriptions of cellular anatomy are not included except in a few cases, as such a study is beyond the scope of this work. It is possible, but not probable, that differences which would be of taxonomic importance might be confined to such minute structures.

The *Pleuroceridae* are streptoneurous gastropods and are placed in the order Ctenobranchiata (Pectinibranchia, Monotocardia) because of the presence of a pectinate gill or ctenidium as the chief respiratory organ. They are placed in the suborder Platypodo owing to the presence of a flat creeping foot. They are assigned to the super family Taenioglossa owing to the possession of a taenioglossid radula consisting of three teeth on each side of the median tooth. The *Pleuroceridae* are placed next to the family *Pomatiopsidae* and form the last family of the subclass Streptoneura as arranged by Baker (1928).

The animals used in this work were identified as *Pleurocera canaliculatum undulatum* (Say) by Mr. Calvin Goodrich of the University of Michigan. However, he says, "it should be understood that, in reality, it is doubtful that it *(undulatum)* is of subspecific value" (personal communication). The term *undulatum* is used more as a conveniece to separate this form from closely related forms, the relationships and values of which have not been fully worked out. To quote Mr. Goodrich again (1922):

> The variability of the Pleuroceridae is notorious. Because of this. . . the family has been neglected. . . That collection of individuals in the Pleuroceridae may be called a species whose predominant characters are not the predominate characters of another colections of individuals.

Material

The animals used in this work were collected at Butler, Kentucky from the Licking River, a shallow stream with a fairly swift current in the main channel.

As far as can be determined from examinations of the contents of the alimentary canal these gastropods are entirely herbiverous. However, here, as in most American fresh water gastropods, there *is* little available *data* on exactly what constitutes the food of these animals.

Nothing is known concerning the breeding activity or eggs of this species. Judging from five other species of this family in which eggs have been recorded, it is probable that the eggs of *Pleurocera canaliculatum undulatum* (Say) will be found on the under side of algae-covered rocks in running water. They will probably be in very small groups of six or eight eggs enclosed in a very convex mass of jelly.

General

The body of the animal is divided into head, foot and visceral mass, as in most gastropods, and is connected to the heavy shell by a large columellar muscle. The mantle is present and encloses in its cavity certain structures which will be discussed below. Various pallial organs can be seen through the mantle in some specimens, the visibility depending upon the amount of pigment present. Usually the osphradium can be seen indistinctly on the extreme left side; at its right side is located the ctenidium (Fig. 13, CT), the leaflets appearing as faint transverse lines.

The head is prolonged into a snout which is capable of extreme contraction and expansion. The snout is flattened dorso-ventrally and the greater part of its bulk is composed of muscle tissue. The covering epithelium is of the same type as that which covers the rest of the head and foot. There are many gland cells, most of which are long and narrow as contrasted with the thick flask-shaped cells of the mantle.

The tentacles have the same color as the snout and are covered with the same type of epithelium. The core of the tentacle is made up of connective tissue and muscle tissue, through the center of which runs the large tentacular nerve accompanied by a large blood vessel. There is no definite arrangment of the muscles into layers, although the greatest number of longitudinal fibers is found in the center. It is probable that these are used to withdraw the tentacles while the remaining, more or less circularly arranged fibers, with the aid of the blood, are used in extending the organ.

The foot is composed mainly of one large mass of muscular tissue covered by general body epithelium. The pedal muscle mass is continuous posteriorly with the columellar muscle. The foot, which forms the main mass of the extruded animal is approximately square in outline and is a dark grey in color.

On its posterior dorsal surface the foot bears the small horny operculum (Fig. 1.).

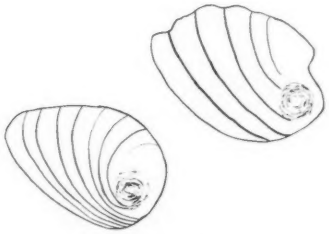


Fig. 1.
Opercula of
Pleurocera canaliculatum
(Say) x4

In sections, the sole of the foot is seen to be covered by a thick carpet of medium length cilia. Beneath the surface and composing part of the ventral epithelium are numerous gland cells which reach greater abundance here than anywhere in the body. There is a wide region just beneath the epithelium which is made up entirely of gland cells. The abundance of well developed cilia and gland clls indicates that probably they play no small part in the locomotion of the animal (Copeland, 1919, 1922). From observations on the movement of the animal it would appear that movement might be due to both muscular and ciliary action, although there is no experimental evidence to support this statement.

Mantle

The mantle is comparatively thin but is bounded anteriorly by a thickened, smooth margin which is slightly recurved to fit against the peristome of the shell. The mantle is covered above and below by cuboidal epithelium, and below also by gland cells which are abundant in some regions, such as ventral to the rectum and in the extreme posterior end of the pallial cavity. The center of the mantle is composed of connective tissue and muscle tissue through which run a large number of blood spaces, which ultimately empty into the afferent branchial sinus.

The osphradium is located on the roof of the pallial cavity just to the left of the ctenidium (Fig. 13,0) and is thus directly in the path of the respiratory current. In gross structure it is little more than a faintly corrugated, low ridge which is slightly darker than the surrounding tissue. Earlier workers and even some of the present workers call this organ an accessory or rudimentary gill. Lacaze-Duthiers (1859) was the first author to doubt the respiratory nature of this structure and finally came to the conclusion that the osphradium was sensory in nature. Because of his work it was known as Lacaze-Duthier's organ. Spengel (1881), who made a comparative study of the organ, came to the same conclusion as Lacaze-Duthier and called it the "Geruchsorgane." It was also known for a time as Spengel's organ. Spengel, speculating as to its function decided that from its position in the mantle cavity near the ctenidium it served for testing the physical and chemical qualities of the water and might possibly aid in selecting food. Bernard (1890) in his anatomical

study of the organ supports the view of Spengel. Copeland (1918) working on two species of marine shells conducted experiments which proved, without much doubt, that these snails found food through directed movements resulting from stimulations of the osphradium by odorous material directed by the shifting siphon.

In *Pleurocera canaliculatum* the osphradium is located in the mantle cavity immediately to the left of the ctenidium where it is in the direct path of the respiratory current. From its structure it would seem impossible for it to have any respiratory value. In cross section the osphradium is a low flattened ridge, the core of which is composed of the large osphradial nerve and supportive tissue through which run a few blood spaces. The epithelium is composed of three kinds of cells, *viz.*, (1) non-ciliated or sensory cells, (2) ciliated cells and (3) glandular cells. The non-ciliated cells occupy the entire flat top of the organ and parts of the sides and are by far the most abundant type. The ciliated cells are found only on the sides of the ridge and cilia are very feebly developed. The gland cells are rather scarce and their distribution is not limited.

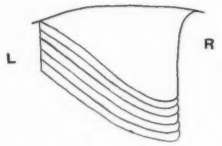


Fig. 2.
Sketch showing shape of ctenidial leaflets. L. left; R. right. x15.

The ctendium hangs from the roof of the pallial cavity, its anterior end lying about the midline anteriorly and extending diagonally posteriorly to the pericardium (Fig. 13). It is composed of about 110 triangular plates which are attached along the base and have rounded apices (Fig. 2). The free sides of the plates are of unequal lengths, the left side being longer than the right side (Fig. 2). The plates are largest in the middle of the ctendium and decrease in size toward each end. The ctendium is of the monopectinate type, the plates being attached in a single row along the ctenidial axis.

In cross section (Fig. 3) each plate is seen to be covered by a layer of epithelium which overlies a thin layer of connective tissue and muscle fibers. In the center of each plate is a blood space through which the blood passes while being aerated. The epithelium, like that of the osphradium, is composed of three types of cells, *viz.*, (1) non-ciliated cells, (2) ciliated cells and (3) gland cells, all of which are columnar. Most of the general surface is covered with non-ciliated cells. All of the cells lie on a very thin basement membrane in which only a few scattered nuclei can be seen and no cell boundries are visible. Just inside this is a layer of connective tissue and muscle fibers which line the blood space. A number of these very fine muscle fibers cros the blood space in an oblique fashion. Prashad (1925) in his discussion of *Pila globosa* says:

> Apparently these muscle fibers, by their contraction, draw together the two surfaces of the lamellae thereby reducing the lacunar spaces and forcing the blood from the lacunae into the efferent vessels.

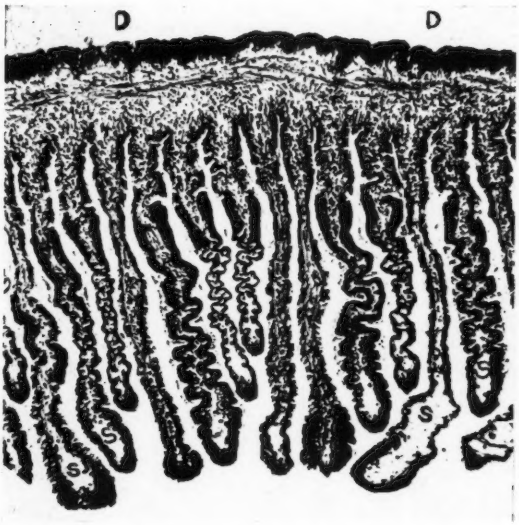


Fig. 3. Photograph of longitudinal section of a portion of the ctenidium, showing cross sections of the ctenidial leaflets. D, dorsal side of the mantle beneath which may be seen a layer of longitudinally arranged muscle fibers above the base of the leaflets; S, blood spaces in the leaflets.

Respiration in this animal is true aquatic respiration for the most part, the blood being aerated in the blood sinuses in the ctenidial plates which hang down in the respiratory current.

It is quite probable that a certain amount of respiration occurs over the general body surface. The mantle is extremely vascular and the walls separating the blood spaces from the water are thin enough for respiratory changes to take place. Also in the periphery of the foot there is a great plexus of blood spaces just beneath the surface and it is probable that some respiration occurs here.

The animals can also carry on respiration for a considerable time in the absence of surrounding water. Along the banks of the Licking River after the water had receded, sometimes hundreds of them would be found in a small pool not over an inch deep and in which the water had been heated to a high degree by the sun. Others have been taken from the surface layer of dried mud which according to the government records of the Licking River, had been out of the water for at least four weeks. If the apertures of the shells were turned down in the dried mud the animals would be found alive and would be active within a few minutes after being placed in water. How-

ever, if the apertures were turned up so the sun could strike the animal they were always dead. In these cases of trapped animals it is probable that their ability to survive is due to their ability to live on a small amount of oxygen rather than by obtaining their full supply by aerial respiration as in the case of some amphibious gastropods.

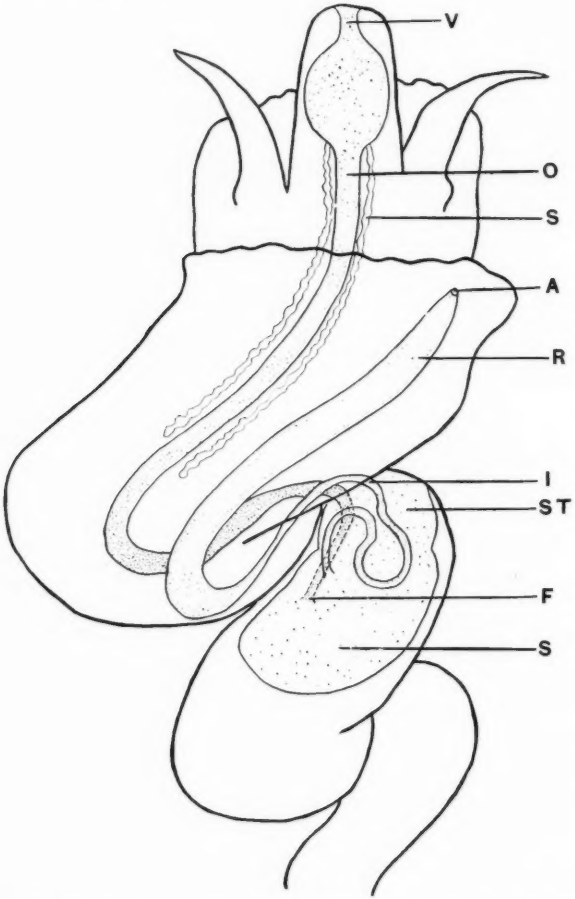


Fig. 4. Outline drawing of entire animal showing dorsal view of alimentary canal. A, anus; F, opening of oesophagus into stomach; I, intestine; O, oesophagus; R, rectum; S, salivary glands; ST, style-sac; V, vestibule; W, stomach.

Alimentary Canal

The mouth is a narrow vertical slit situated at the anterior end of the snout and remains closed unless the animal is feeding. The vestibule, (Fig. 4,V) a short narrow passage, connects the mouth cavity with the pharyngeal cavity. Posteriorly the pharynx opens into the relatively small oesophagus which appears flabby in contrast to the muscular buccal mass. The oesophagus continues straight posteriorly through the perivisceral cavity to enter the visceral mass and empty into the stomach on the ventral side (Fig. 4, F).

There are two salivary glands which lie on either side of the anterior part of the oesophagus (Fig. 4, S). These glands are long, slightly convoluted tubes of a light yellow color. They become smaller at the extreme anterior end to form short ducts which pass through the nerve ring to enter the muscles of the buccal mass and open into the pharynx at this point.

The stomach is in contact with the liver and gonad posteriorly and it is bounded by the style-sac and the intestine anteriorly. The oesophagus opens into a deep groove on the left side of the stomach about one third the way from the anterior end. Immediately posterior to the oesophageal opening and also opening into the groove just mentioned is the single duct from the digestive gland. The roof of the stomach presents a corrugated appearance because of the many low parallel ridges. From the floor of the stomach a number of folds project into the cavity which are really folds of the stomach wall

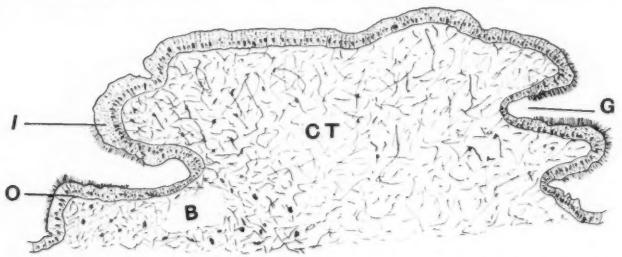


Fig. 5. Cross section of gastric folds in floor of stomach. B, blood vessel; CT, connective tissue; G, groove or gutter between outer and inner gastric folds; I, Inner gastric fold; O, outer gastric fold.

and are called gastric folds. The largest, which is the central or inner fold, is pyriform in outline with the broadest end being posterior and gradually narrowing anteriorly to where it ends at the right anterior end of the stomach. The width of the top of the central fold (Fig. 5. I) is slightly greater than the width of the base, so that its upper edges overhang to a slight extent. Lying immediately next to the central fold is a much narrow outer fold, which originates at about the middle of the left margin and runs as a ridge around the inner fold along the left, posteriorly and partly on the right side. Due to the proximity of the outer and inner gastric folds, there is formed between the two a narrow deep gutter which is continuous with the groove into which the

oesophagus and digestive gland duct empty. On the left posterior margin of the stomach there originates a narrow lateral fold which runs directly cephalad to bend sharply on itself, the second limb being internal and parallel with the first, so that a groove is formed between the two. The second limb ends near the opening of the oesophagus and digestive gland duct which lies near the beginning of the gutter between the outer and inner gastric folds. It would appear that the function of these folds is to direct the food contents of the stomach and to aid in their thorough mixing.

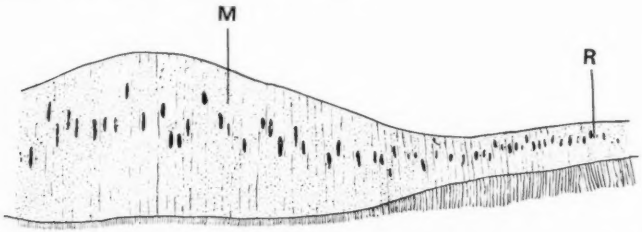


Fig. 6. Tall cells making up the longitudinal ridge on the style-sac aspect of the major typhlosole. Note the length of the cilia on these cells (M) as compared with those of the cells lining the rest of the style-sac. x215.

In the right anterior portion of the stomach the epithelium develops a cuticular lining, the thickest portion of which lies opposite the opening of the style-sac, which will be described below, and is termed the gastric shield (Fig. 7). This is a slightly flexible, iridescent, irregular structure. Its shape is somewhat like a flat oblong plate which has been bent in a spiral fashion to form an incomplete tube. The lower edge fits beneath the margin of the inner gastric fold. The thick shield does not extend to the dorsal wall, but a thin cuticular continuation does extend halfway across the anterior roof.

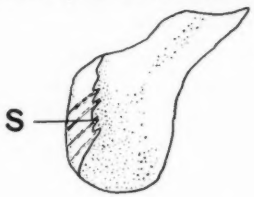


Fig. 7.
Gastric shield as seen from a dorsal view. S, spines on the left margin. x30.

Directly in front of the stomach there is the style-sac, a chamber about three-fourths as long as the stomach. It is oblong in outline and has very thick walls, darkly pigmented. The style-sac as the name suggests, contains the crystalline style which projects through the circular opening into the stomach to fit against the gastric shield.

Along the left side of the style-sac and by a slit with it into the stomach is a narrow groove which is really the beginning of the intestine. This groove

is anatomically in communication with the style-sac through all of its length, but functionally it is separated by opposing ridges or typhlosoles which are approximately dorsal and ventral in relation to each other. There is not so much difference in size between the two typhlosoles although the dorsal is perhaps the larger and the ventral the broader. The dorsal is more or less pointed on its lower edge and this keel fits into a corresponding groove on the ventral typhlosole, so that the cavities of the groove, which is called the intestinal groove, and the style-sac are actually separate (Fig. 8).

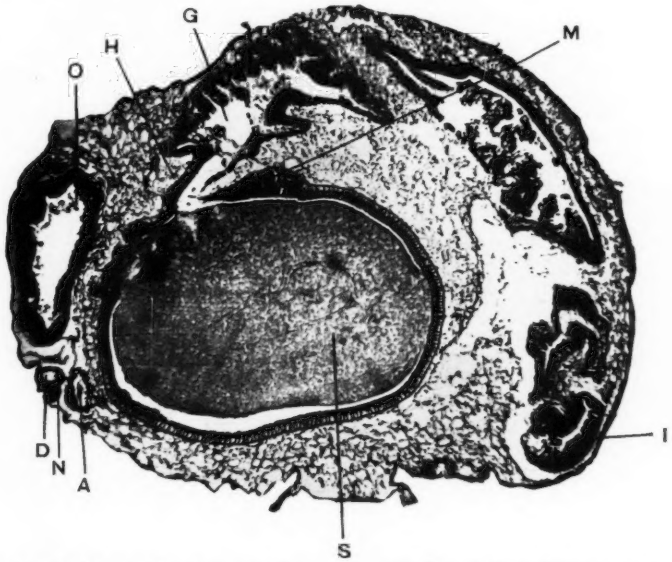


Fig. 8. Photograph of cross section of the crystalline style in the style-sac and adjacent structure. A, visceral artery: D, genital duct; G, intestinal groove; H, minor typhlosole; I, intestine; O, oesophagus; M, tall row of cells located on the style sac aspect of major typhlosole; N, nerve from visceral ganglion; S, crystalline style.

The digestive gland which occupies the apex of the visceral mass is in contact with and completely covered by the gonad except for the very tip of the spire and a band along the columellar margin on each side of the genital duct (Fig. 17). The gland consists of a large number of tubules which vary in size and are bound together by connective tissue. The smaller tubules unite to form larger tubules which ultimately empty into the large duct which leads to the stomach and opens into the gastric cavity by a single opening (Fig. 9, B).

The intestine continues from the anterior end of the intestinal groove, passes in a loop over the syle-sac back to the left side (Fig. 4, I) where it

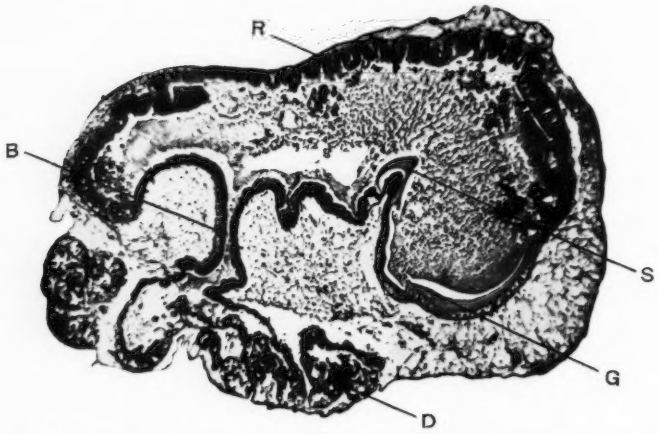


Fig. 9. Photograph of cross section of the stomach showing entrance of the single duct from the digestive gland. B, entrance of the digestive gland duct; D, the most anterior part of the digestive gland; G, section of the ventral part of the gastric shield; R, low folds on roof of stomach; S, section of one of the spines of the left margin of the shield.

then curves to the right and forward to continue as the rectum. This latter organ passes anteriorly in the mantle to end in a small anus on the right side of the pallial cavity. The rectum is marked by many oblique transverse grooves, and it is in these grooves that the fecal pellets are formed.

Histology of the Alimentary Canal

The "lips" and the margin of the mouth are covered by a low columnar epithelium similar to that covering the general body surface. Just inside the mouth the cells are very narrow and their height in at least twice that of the cells just outside the mouth. The nuclei are prominent and are located at various levels so as to produce a pseudostratified appearance. This area also has an unusually large number of gland cells. The epithelium lining the vestibule is peculiar in that it is covered by a thick cuticular border and is entirely devoid of gland cells. The cavity of the pharynx is irregular in shape and varies at different levels. Likewise the character of the lining epithelium varies from tall columnar to low cublidal in different regions.

The salivary glands, of which there is a single pair, are round in cross section (Fig. 10, S). Each is a long unbranched, slightly convoluted, simple tube. Often one gland is slightly longer than the other. The cells making making up the walls of the glandular part are tall, irregular, darkly staining cells, which bear a very few small scattered cilia. The bases of the cells rest on a delicate basement membrane.

The walls of oesophagus is composed of the epithelium lining the lumen and a surrounding muscular layer. The latter is not divided into distinct longitudinal and circular layers but the fibers are arranged in an irregular fashion. It may be said that the muscular layers of the whole intestine are poorly developed. The cells lining the oesophagus are tall columnar cells of two kinds—glandular and ciliated cells, of which the former greatly outnumber

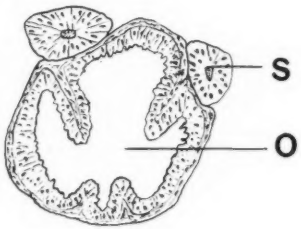


Fig. 10.
Cross section of oesophagus and salivary glands showing the shape of the oesophageal cavity. O, lumen of the oesophagus; S, salivary gland. x100.

the latter. In fact, the oesophagus contains a larger proportion of glandular cells than any other portion of the gut. The ciliated cells are very irregular in shape and the components of the cells are usually vague. In cross section, the lumen of the oesophagus is seen to be partly divided into three main parts by two pairs of longitudinal ridges (Fig. 10). Extending from the dorsolateral region on each side, beneath each salivary gland is a septum which extends ventrally about one half way across the cavity. Extending dorsally from the floor, immediately on each side of the midline of the oesophagus, is a pair of comparatively low ridges with a narrow groove between them (Fig. 10). These septa become less prominent posteriorly, until immediately anterior to the stomach the oesophagus presents many low longitudinal striations.

The stomach is covered with a thin layer of connective tissue and muscle fibers, the latter having no regular arrangement into layers. The inner wall of the stomach is lined with ciliated epithelium similar to that found in other parts of the gut, except it is not so tall and fewer gland cells are present. Opposite the opening of the style-sac the epithelium acquires a cuticular covering which forms the gastric shield (Fig. 7). The shape of the shield as described above is somewhat spiral. The left margin of the shield curves dorsally to terminate in a sharp edge which bears on an average of six pointed teeth or spines. These spines are continued on the outer wall of the shield as ridges which fade out ventrally. The posterior semi-liquid end of the style fits against the shield.

The cells underlying all the cuticular structures stain less than the other gastric spithelial cells, and are very much taller and narrower. These cells, of course, bear no cilia, this being the only large expanse of the alimentary canal epithelium which does not. The epithelium covering the sides of the gutter formed by the outer and inner gastric folds is the most abundantly ciliated of any found in the stomach, the cells covering the top of the inner fold having

no cilia at all (Fig. 5). The cilia on the floor and roof of the stomach are only weakly developed.

The digestive gland, yellowish brown in color, is composed of one undivided lobe consisting of a large number of tubules, the blind ends of which seldom reach the surface except on the columellar side because of the overlying gonad (Fig. 17). The tubules are bound together by connective tissue

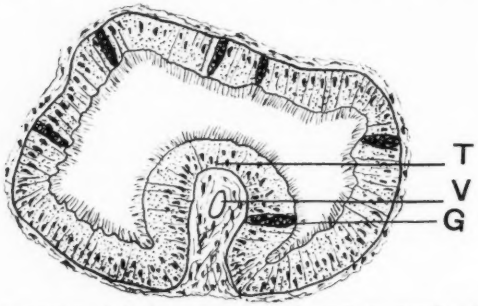


Fig. 11. Cross section of the intestine showing the well developed typhlosole (T); G, gland cells; V, blood vessels. x100.

in which there are many blood spaces. The tubules, which are more or less circular in cross section, are lined by two kinds of cells—gland cells and ferment cells, the latter being more numerous. One or more vacuoles are often present in these cells and they usually contain from one to six large bodies known as secretory bodies. These bodies are solid, rounded and from dark brown to black in color. The gland cells are not so broad as the ferment cells and are more circular in shape. The cytoplasm is finely granular but in general does not stain so deeply. The products of the gland ultimately pass to the single duct on the columellar side which opens into the floor of the stomach directly posterior to the opening of the oesophagus (Fig. 9, B). This opening and the proximal part of the duct are lined with ciliated epithelium similar to that region of the stomach.

The style-sac is lined with columnar cells which bead cilia which are strikingly developed and are all exactly the same length. The proximal ends of the cilia appear to be fused so that in sections there is a narrow border adjacent to the inner ends of the cells. The cells stain rather lightly and are vacuolated. In the dorsal region, these epithelial cells contain a large amount of pigment matter in the form of crowded black granules located in the distal half of the cell. No typical gland cell are present in this epithelium. On the style-sac aspect of the major typhlosole there is a longitudinal ridge of very tall cells extending almost the whole length of the style-sac. These cells are not vacuolated, contain no pigment, and bear short cilia (Fig. 6). This ridge projects only slightly above the surrounding level on the inner surface of the sac, and as the cilia are shorter than the cilia borne by the adjacent cells, the

level formed by the distal ends of the cilia is unbroken. Toward the intestinal groove the cells become low columnar in character rather abruptly, are weakly ciliated on the major typhlosole, and gradually take on the appearance of the characteristic intestinal ilning.

The epithelial covering of the minor typhlosole is made up of tall columnar cells with elongate nuclei, darkly staining cytoplasm and are strongly ciliated, no gland cells being present. The transition to intestinal epithelium is rather gradual. The intestinal groove is lined by typical gut ejithelium.

The crystalline style agrees in general with that described for other forms. It is about 1.5 mm. long and 0.7 mm. thick, round with blunt ends, the ends toward the stomach being in a semi-liquid condition and mixed with the stomach contents (Fig. 12). In a normal animal it completely fills the style

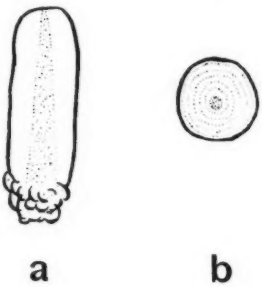


Fig. 12a.
Lateral view of the crystalline style showing food core; b. end view of crystalline style showing the coaxial layers. x15.

sac. In optical section the whole structure is seen to have a definite spiral arrangement, the spiral being from left to right from the anterior to the posterior end. In a fresh style there is a distinct opaque core, the "food core" of some writers. The core is thickest at the posterior end and gradually narrows to a thin thread at the opposite end. The posterior semi-liquid end projects into the stomach and fits against the gastric shield, practically filling the anterior end of the stomach.

The consistency and color of the style vary greatly. In a supposedly healthy animal it is in the form of a rod varying from a clear transparent to a smoky bluish color. There is some evidence that temperature or food supply and possibly oxygen supply may have some effect on the style. In animals kept for some time at a temperature of 3 degrees centigrade the style is a brownish color and the periphery is in a semi-liquid condition. I have never found a living animal with the style absent. On the other hand I have never found a style in a preserved animal (Magruder, 1935). If a fresh style is removed and placed in 95% alcohol, it coagulates almost immediately, which suggests an albuminoid nature as has indeed been found to be the case by other workers on other animals. If a style is removed and placed in water it completely disappears in 20 minutes or less, the core being the first part to disappear. A crystalline style was not known to occur in any member of the Pleuroceridae until recently when it was recorded as occurring in *Pleurocera*

canaliculatum undulatum (Say) and *Lithasia obovata* (Rafinesque) (Magruder, 1935). It is probable that further investigation will disclose the presence of a style in other species of this family.

Beyond the intestinal groove, in the coils of the intestine, the lining epithelium is esentially the same as that in the intestinal groove. In this region however, a marked typhlosole is present (Fig. 11, T) covered by cells which are taller than those forming the remainder of the lining. This part of the intestine contains gland cells but they are not nearly so abundant as in the intestinal groove and oesophagus.

There is a gradual transition from the comparatively small intestine to the wide transversely folded rectum which lies in the mantle. The muscular layer is practically absent in the wall of the rectum. The cells composing the lining epithelium are very regular low columnar cells with cilia well developed. Gland cells are present but are not very abundant, the largest number being near the anus.

The Vascular System

The pericardial cavity is located on the left side of the body whorl at the extreme posterior end of the mantle cavity, and is visible after removal of the shell. The pericardium is approximately square in outline and its posterior end extends for a short distance beneath the posterior renal organ as a narrow tube-like extension. The pericardial wall is composed of one layer of low cuboidal cells resting on a thin structureless membrane through which the heart can be seen in the pericardial cavity.

The heart has one auricle and one ventricle, the auricle being anterior to the ventricle (Fig. 13, R). The auricle is a thin walled white sac approximately 0.9 mm. in length, somewhat oval in outline with the broadest end anterior. Into the anterior end of the auricle opens the large efferent ctenidial sinus and the smaller efferent renal sinus, these being the only vessels which bring blood directly to the heart. Posteriorly the auricle is separated from the ventricle by a marked constriction through which passes the short auricular-ventricular canal. I can find no valves in this region guarding the opening between the two chambers such as have been described for some other monotocardia.

Externally the auricle is covered by a thin almost structureless endothelium-like layer of protoplasm in which nuclei can be distinguished but no cell walls. I can find no lining of any sort inside the auricle or ventricle, the muscles appearing to project directly into the cavity. The auricular wall is comparatively thin and is composed of loosely arranged, variously sized bands of muscles. The cavity of the auricle appears small because of the many bands of muscle fibers extending from the walls. As a result, the auricular cavity appears sponge-like with many irregular deep pockets rather than as one clear-cut cavity.

Entering the auricle anteriorly with the efferent renal sinus is a nerve, a

branch from the visceral ganglion. It enters the right auricular wall, passes posteriorly a short distance and divides into two branches of equal sizes which can be traced as far posteriorly as the anterior end of the auricular-ventricular canal.

The ventricle is pyriform in shape, about 1.5 mm. in length, located immediately posterior to the auricle. Originating from the posterior end of the ventricle is a short aortic trunk which immediately divides into two main aortic trunks of the body, one going anteriorly and called the cephalic aorta, and the other, the visceral aorta, passing posteriorly.

The ventricular walls are very thick and are composed almost entirely of muscle fibers. Like the auricle, the ventricle is covered by a thin endothelial layer but no inner lining is present, the muscles being exposed directly to the blood. The muscles are grouped into definite bundles of various sizes. The length of none of the bundles exceeds one-third the circumference of the ventricle. A great many of the bundles run more or less transversely and some obliquely but none run longitudinally. The ends of the bundles are usually spread out in a finger-like fashion at each end where they are attached. These bands of muscle give the inside of the ventricle the appearance of having heavy ribs between which are sinuses.

External to this muscular layer is another indistinct layer of muscles made up of an irregular network of branching muscles which run in all directions. The ventricular wall then is composed of a outer endolethial covering, an external thin muscular layer and an inner thick, spongy, muscular layer. No ventricular valves were found.

The cephalic aorta (Fig. 13, C) bends sharply to the left and passes anteriorly along the outer edge of the pericardial cavity. On the posterior side of this arch a large branch is given off which goes posteriorly to the walls of the style-sac. The main trunk of the cephalic aorta leaves the pericardial cavity at the anterior end and passes beneath the efferent ctenidial sinus. It follows an oblique course toward the midline to enter the perivisceral cavity and goes dorsal to the oesophagus and salivary glands and just beneath the floor of the pallial cavity. Just posteriorly to the cerebral ganglia it turns ventrally and passes to the right of the base of the supraintestinal nerve and then ventrally posterior to the right pleural ganglion where it gives off a branch to the buccal mass. This branch then redivides in the buccal mass into posterior and anterior branches. The anterior branch, supplies blood to the anterior part of the buccal mass and sends branches to the snout and lips. The posterior branch, which is larger, is distributed to the radula sac, the anterior part of the oesophagus and the salivary glands. The main trunk continues ventrally between the cerebro-pedal and pleuro-pedal connectives. Just anterior to the pedal commissure, over which it passes, the cephalic aorta divides into a right and left branch each of which divides again into a right and left branch and each of these redivides into an anterior and posterior branch of equal size (Fig. 13). The great expansion of the foot is no doubt aided by the large amount of blood supplied to it through the well developed arteries.

The large visceral artery (Fig. 13, VA) leaves the short aortic trunk to course obliquely toward the right, just beneath the posterior edge of the posterior renal chamber and directly dorsal to the anterior end of the style-sac. When it reaches the genital duct, it turns posteriorly and proceeds back accompanied by the genital duct and a nerve from the visceral ganglion. The

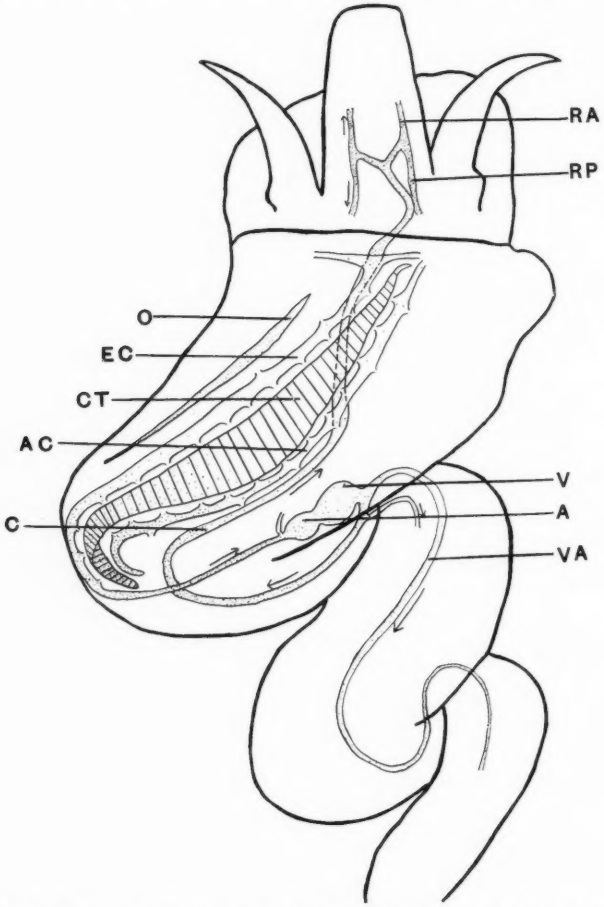


Fig. 13. Outline view of entire animal showing dorsal view of chief arteries and veins. A, auricle; AC, afferent ctenidial sinus; C, cephalic aorta; CT, ctenidium; EC, efferent ctenidial sinus; O, osphradium; RA, right anterior pedal artery; RP, right posterior pedal artery; V, ventricle; VA, visceral aorta.

visceral artery after giving off branches to the posterior part of the stomach and anterior part of the digestive gland and gonad, ends in the apex of the gonad and digestive gland.

The blood which is distributed by the arteries is collected into many small excavations or sinuses in the tissues. The venous system is composed largely of these spaces or sinuses which usually lack definite walls and consequently are hard to define since they have no definite pattern.

The foot is one of the most vascular organs in the body. The blood from the large pedal artery finally enters the plexus of sinuses in the periphery of the foot and these are so numerous as to give the foot a spongy apparance in sections. The blood is returned by way of the pedal sinus to the center of the foot, then dorsally into the perivisceral sinus into which it empties. The blood is probably aided in its circulation in the foot by movements of the pedal muscles. They almost always show some movement even when the animal is at rest.

The perivisceral sinus lies below the floor of the pallial cavity and above the foot, surrounding the anterior part of the alimentary canal. The blood enters this sinus from the pedal sinus, head and surrounding parts. From there the blood goes to the anterior renal organ and through the mantle directly to the afferent ctenidal sinus, or through the mantle to the afferent ctenidial sinus directly.

The periintestinal sinus lies for the most part on the columellar side of the animal and collects blood from the stomach, style-sac, digestive gland and genital system. Part of the blood returns by way of the anterior renal organ to the afferent ctenidial sinus, and part by way of the posterior renal organ to the efferent renal sinus, thence to the heart.

The branchial sinus is a collection of sinuses in the mantle region which eventually form the definite afferent ctenidial sinus lying along the right margin of the ctenidium. Surrounding the rectum is the large rectal sinus which collects blood from parts of the mantle, genital folds and the surrounding region. Part of this blood may continue directly to the afferent ctenidial sinus and part, by way of the anterior renal organ, to the afferent ctenidial sinus. The afferent ctenidial sinus sends a small branch into each ctenidial platelet where the blood is aerated in the thin walled platelets. The blood is collected from the ctenidium by the efferent ctenidial sinus which lies along the left margin of the ctenidium and just to the right of the osphradium from which it also collects blood. This sinus passes directly posterior to enter the auricle.

In the dorsal part of the posterior renal organ is a comparatively small sinus, the afferent renal sinus, which collects blood from the rectal region and terminal part of the intestine. This afferent renal sinus breaks up into a large number of small branches, thus forming a renal portal system. The blood from this plexus is collected by the efferent renal sinus which opens into the auricle. The blood going through this system is, of course, not aerated in the ctenidium so that the blood in the heart is mixed.

Summary of Blood Circulation:—The blood passes from the ventricle to

part of the style-sac, the head, part of the mantle, oesophagus, buccal mass, foot and associated organs by way of the cephalic aorta. The blood is carried to the digestive gland, stomach, gonad, part of the style-sac, and related organs through the visceral aorta and its branches. Blood from various parts of the body is finally collected into two main sinuses—the perivisceral and perintestinal sinuses, from which it returns to the heart by one of three general routes: (1) directly to the afferent ctenidial sinus by way of the perirectal and the mantle sinus, and through the ctenidium to the efferent ctenidial sinus, thence to the auricle; (2) through the anterior renal chamber and to the afferent ctenidial sinus to follow the same route; (3) to the posterior renal organ by way of the afferent renal sinus, through the renal plexus to the efferent renal sinus into the auricle without aeration.

Nervous System

In general, the nervous system of this species is similar to that described for other streptoneurous gastropods. In the following account I have not gone into detail concerning the terminology of the different ganglia and nerves. This has been adequately discussed by Spengel (1881) and by Bouvier (1887) in his memorable work on the nervous system of the prosobranchs. The names which I have used for the main ganglia are the generally accepted names of Spengel, such as cerebral, buccal, pedal, pleural, supraintestinal, subintestinal and visceral. The nervous connections between like ganglia of opposite sides are called commissures and the connections between unlike ganglia of the same or opposite sides are called connectives.

In th drawings of the nervous system (Figs. 14 & 15) only the main nerve trunks are shown. It is not practical to show the many small branches which vary a great deal as to size, number and relative position and can not be shown in proportion in a drawing of this size.

The paired cerebral ganglia are connected with each other toward their posterior ends by a short thick commissure which passes dorsal to the oesophagus (Fig. 15, CC). Each ganglion is roughly oval or pear-shaped with the later aide being the longest. The anterior end of each ganglion is pointed where it gives off several large nerves to the anterior head region. The posterior end lies directly dorsal to the extreme anterior end of the pleural ganglia.

The cerebral commissure is short, thick and rather wide, the narrowest part being in the middle. It varies somewhat in length. In some animals it is so short that the two cerebral ganglia appear to be fused in the midline.

Each cerebral ganglion is connected to the buccal ganglion of the corresponding side by a small cerebro-buccal connective. This originates on the antero-ventral side of the cerebral ganglion and passes anteriorly to connect with the buccal ganglion at the postero-lateral end.

Each cerebral ganglion is connected to the pedal ganglion of that side by a long round cerebro-pedal connective which arises on the ventral side of the cerebral ganglion and passes ventrally to the dorsal side of the pedal ganglion. These cerebro-pedal connective often show a variable number of enlargements along their course which appear superficially to be ganglia, but a study of their

internal structure shows them not to be such. Each cerebral ganglion is connected with the pleural ganglion of the same side by a short connective.

The nerves arising from the cerebral ganglia are identical on the two sides, therefore the branches of only one side will be described.

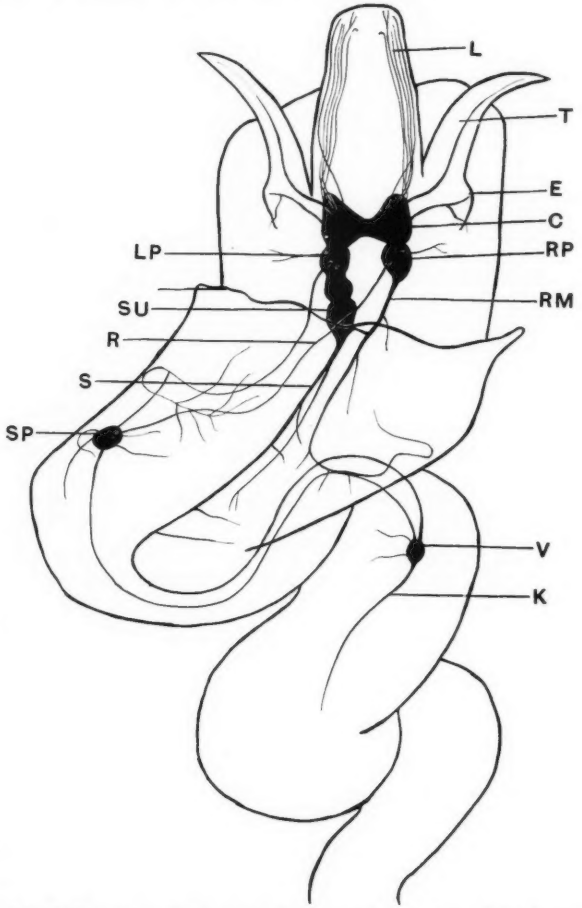


Fig. 14. Outline view of entire animal showing dorsal view of chief nerves and ganglia in situ. C, cerebral ganglion; E, eye and optic nerve; K, visceral nerve; L, labial nerves; LP, left pleural ganglion; R, supraintestinal nerve; RM, right mantle nerve; RP, right pleural ganglion; S, subintestinal nerve; SP, supraintestinal ganglion; SU, Subintestinal ganglion; T, tentacular nerve; V, visceral ganglion.

Anterior Nerves

1. A medium sized labial nerve (Fig. 15, CI) arise from the antero-dorsal side of the cerebral ganglion and courses laterad to the dorsolateral side of the perivisceral cavity, where it follows along the ceiling of the cavity, being attached to the wall by connective tissue as well as by small nerves which branch to the muscles of the snout. This nerve terminates at the anterior end in the muscles at each side of the mouth opening.

2. A large labial nerve (Fig. 15, C2) arises on the antero-dorsal surface near the anterior part of the cerebral ganglion. Its point of origin is slightly lateral and anterior to that of the first labial nerve. It continues obliquely forward along the wall of the cavity ventral to the nerve described, around the buccal mass, giving off many smaller branches to the snout muscles and finally distributed in the region of the lips.

3. The third labial nerve (Fig. C3) arises directly lateral to the second labial nerve, and is about the same size. In some cases the origins of the second and third labial nerves are fused so that they appear as branches of a single nerve. This nerve passes anteriorly parallel with the other labial nerves to the middle of the snout, where it passes ventrally beneath the buccal mass and terminates in the ventral lip region.

4. The pharyngeal nerve, (Fig. 15, C4) originates at the anteroventral end of the cerebral ganglion and passes forward along the floor of the perivisceral cavity. It curves sharply mediad at the level of the anterior end of the buccal mass to enter this organ where it is distributed to the anterior muscles of the buccal mass.

5. The fourth labial nerve is the only remaining nerve arising from the anterior end of the cerebral ganglion. It originates just ventral to the pharyngeal nerve and passes anteriorly, parallel with it. Its anterior end terminates in two branches of the same size, one going to the lip region and the other to the muscles of the ventral side of the buccal mass.

Lateral Nerves

1. The large tentacular nerve (Fig. 15, T) arises on the dorsal side of the cerebral ganglion on the antero-lateral surface. This is the largest nerve originating from the cerebral ganglion. It goes laterally to where it enters the muscles, and then obliquely forward to the base of the tentacle where it nters the tentacular tissue, giving off many small branches along its route to the end of the tentacle.

2. The optic nerve (Fig. 10, O) is second in size only to the tentacular nerve described above. The optic nerve arises from the ventro-lateral side of the cerebral ganglion and enters the muscles of the wall of the perivisceral cavity to go directly to the eye located at the outer base of the tentacle. The optic nerve usually, but not always, gives rise on its posterior side to a small nerve to the muscles in the region immediately posterior to the eye.

3. The small statocyst nerve originates from the ventral side of the cerebral ganglion at its posterior end. It passes directly ventrally, just anterior

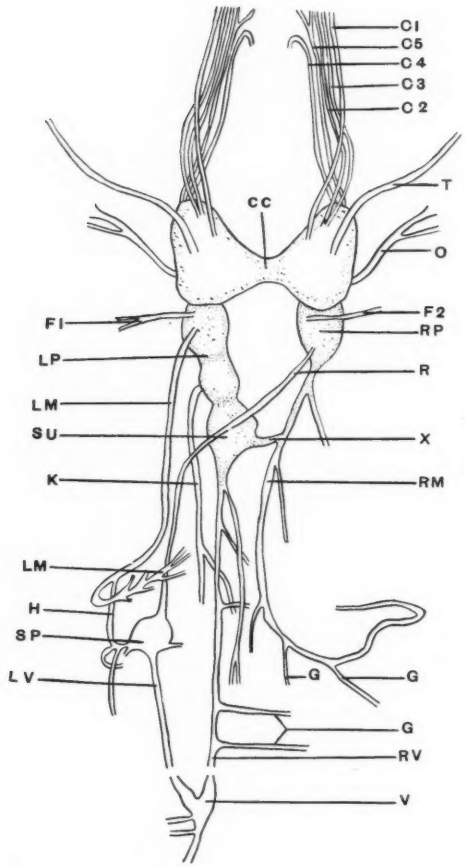


Fig. 15. Dorsal view of nervous system. C, cerebral ganglion; C1, C2, C3, C4 and C5, nerves originating from anterior end of cerebral ganglion and innervating the lips, snout and anterior end of the alimentary canal; F1 and F2, nerves originating from the left and right pleural ganglia innervating muscles of neck region; G, genital nerves; H, Connection between left mantle nerve and supraintestinal ganglion; LM, left mantle nerve; LP, left pleural ganglion; LV, left visceral connective; O, optic nerve; R, supraintestinal nerve; RM, right mantle nerve; RP, right pleural ganglion; RV, right visceral connective; SP, supraintestinal ganglion; SU, subintestinal ganglion; T, tentacular nerve; X, connection between subintestinal ganglion and right mantle nerve.

to the cerebro-pedal connective, passing to the outside obliquely across the pleuro-pedal connective to terminate in the wall of the statocysts, which are located at the posterior dorsal end of each pedal ganglion.

The round buccal ganglia are paired and lie just ventro-lateral to the anterior end of the oesophagus, anterior to, and slightly above the level of the tip of the radula sac. They are connected by a long thick commissure whose diameter is approximately half that of the ganglia. The buccal ganglia and connectives are entirely covered by the tissue of the buccal mass and cannot be seen until dissected out of this region. A very small nerve originates from each ganglion and continues anteriorly to end in several twigs which supply the posterior part of the buccal mass. One branch, however, goes to the anterior part of the buccal mass. All of these nerves arise from one nerve trunk originating from each ganglion.

The paired pedal ganglia are oval in shape and are ocnnected by a single short thick commissure. Dorsally the pedal ganglia are connected to the cerebral ganglia by the long cerebro-pedal connectives and to the pleural ganglia by the pleuro-pedal connectives.

From each pedal ganglion there arise two large nerves, one anterior, the other posterior. Besides these, there ar usually sveral small irregularly arranged nerves which are not constant in their appearance. The anterior nerve is distributed anteriorly through the pedal muscles and gives off many branches which rebranch in their turn. There is no regularity in the number or pattern in these branches from the anterior pedal nerve.

The posterior pedal nerve is about the same size as the anterior pedal nerve and is distributed posteriorly beneath the opercular region of the foot. From it originates many branches, which as in the case of the anterior nerve, follow no definite pattern. The number of nerves originating from the anterior and posterior pedal nerves is large, making the foot one of the most thoroughly innervated organs of the body.

The pleural ganglia (Fig. 15) are paired but not similar in shape nor are the nerves which arise from them symmetrically arranged. These ganglia therefore, will be described separately.

The left pleural ganglion lies near the left cerebral ganglion and is connected with it by a short cerebro-pleural connective. This gangion is oblong in shape and superficially it appears to be two ganglia. However, the whole mass is one ganglion separated by a constriction into a larger anterior and a smaller posterior lobe. Posteriorly this ganglion is closely associated with the subintestinal ganglion, being separated from it only by a constriction. The anterior lobe of the left pleural ganglion gives rise to two nerves, the most anterior and smallest of which is a small lateral nerve (Fig. 15, FI) which originates from the dorsal side of the ganglion and passes dorsolaterally into the muscular wall of the perivisceral cavity to supply some of the muscles in the neck region. The second nerve to arise from the anterior lobe of the left pleural ganglion is the left mantle nerve. This nerve originates on the dorsolateral side of the anterior part of the elft pleural ganglion and passes posteriorly on the left side of the oesophagus beneath the left salivary gland. At

the junction of the mantle and neck it gives off a small branch posteriorly which ramifies in the muscle. This small branch meets and fuses with another branch of similar size from the supraintestinal ganglion. The main branch of the left mantle nerve enters the mantle and passes toward the right side in the anterior part of the mantle tissue. The course of this nerve through the mantle is very tortuous, giving off many branches, many of which extend anteriorly to the margin.

The only nerve to originate from the posterior lobe of this ganglion is the columellar nerve. This nerve leaves the ganglion from the center of the lateral side of the posterior lobe and passes posteriorly along th floor of the perivisceral cavity parallel to and to the left of the subintestinal nerve to be described below. At the region of the mantle margin, it enters the floor of the perivisceral cavity to pass to the columellar muscle. It gives rise on its right side to a very small nerve which passes beneath the subintestinal nerve and disappears in the muscles of the floor of the cavity.

The right pleural ganglion is broader than the left and is not divided into two parts as is the left (Fig. 15, RP). Its anterior end projects slightly beneath the right cerebral ganglion and is connected to it by the short vertical cerebro-pleural connective. Three nerves arise from the right pleural ganglion. The most anterior of these (Fig. 15, F2) arises from the dorso-median side and passes directly laterally to terminate in the muscles of the neck. Posteriorly the right pelural ganglion narrows to a point where two large nerves are given off side by side. The most median of these is the large supraintestinal nerve (Fig. 15, R). This nerve passes posteriorly dorsal to the oesophagus and salivary glands and ventral to the cephalic aorta, to the left wall of the perivisceral cavity. Here a medium sized round ganglion is formed lying in the muscular tissue. From this ganglion, which is the supraintestinal ganglion (Fig. 15, SP), are given off several smaller nerves, the total number of which varies in different animals. One of the branches which appears constantly passes laterally to the junction of the body and mantle, where a small secondary branch is given off which passes anteriorly to anastomose with a branch from the left mantle nerve. This anastomosis between these two nerves composes what is known as zygoneury. One or more larger branches pass a short distance through the mantle to the osphardium where they form the large nerve which runs the length of this organ and forms its core. Other nerves belonging to this complex pass to the mantle tissue, mantle margin and the anterior end of the ctenidium, while other smaller branches pass to the parietal wall. The chief nerve arising from the supraintestinal ganglion continues posteriorly to the left of the oesophagus as the left visceral connective.

Originating from the right pleural ganglion immediately lateral and ventral to the supraintestinal nerve is the large right mantle nerve (Fig. 15, RM). This nerve passes posteriorly along the right side of the perivisceral cavity to the right of the oesophagus. At the level of the posterior end of the subintstinal ganglion there is a thick nervous connection (Fig. 15, X) between that ganglion and the nerve being described. At the region of the mantle border the nerve curves to the right and enters the wall of the perivisceral cav-

ity. Just ventral to the right mantle margin a small posterior branch is given off to the anterior part of the genital folds. Soon two larger genital nerves are given off which pass to the anterior and middle parts of the genital folds where they continue longitudinally along the base of the folds. The larger branch goes to the external fold.

The subintestinal ganglion is separated anteriorly from the left pleural ganglion only by a constriction. On the right posterior end originates the thick nervous connection (Fig. 15, X) to the right amntle nerve. Posteriorly the ganglion narrows to form the subintestinal nerve, the only nerve to arise from this ganglion except the connection mentioned above. Several small nerves pass from the main trunk into the muscles of this region. The main nerve passes posteriorly as the right visceral connective to the visceral ganglion. At the level of the posterior end of the genital folds it gives rise on the right side to two or three medium sized genital nerves which pass laterally to terminate in the genital folds.

The two visceral connective pass posteriorly to unite at the visceral ganglion (Fig. 15, V). This is an indistinct "Y-shaped" ganglion which lies dorsal to the columellar muscle, ventral to the kidney and anterior to the stomach. Only one main nerve originates from the visceral ganglion and irregular branches from this ninervate the various oragns of this region. The main trunk (Fig. 14, K) passes posteriorly to the digestive gland, gonad and posterior end of the stomach, parallel with and near the genital duct and visceral aorta.

Sense Organs

Earlier workers called the statocyst the otocyst and the nerve supplying it the auditory nerve. These structures are still referred to as such by some workers. However, Tschachotin (1908), who has investigated this organ in some of the mollusca, has come to the conclusion that the organ is one of equilibrium rather than hearing and that it serves to regulate the animal's position in space. In this animal, as in other gastropods, the statocysts are paired. They are located at the postero-dorsal end of each pedal ganglion and connected to that ganglion by connective tissue which forms a thin envelope around the organ. The cavity is lined by a single layer of low cuboidal cells in which the cell walls are very indistinct. Some of the cells bear small, poorly developed, cilia-like processes on their inner ends. These "cilia" are very sparse and have no definite pattern, many of the cells appearing to have none at all. The cells which do not have any of these "cilia" appear identical in all other respects.

The cavity of the statocyst is almost filled with small clear statocontia which are transparent. The number of statocontia varies in different animals and even in the two sides of the same animal. There are usually from 30 to 40 in each statocyst. One or two statocontia may be larger than the others, the large one being in the center with the others arranged around it. The average shape may be described as "barrel-shaped" and in the case of the larger

ones there are faint longitudinal striations which increase the resemblance to a barrel. A few of the statocontia may be cigar-shaped and a few small ones are round. When dilute HCl is applied, they dissolve with effervesence.

The eyes are located at the outer bases of the tentacles. Microscopically the eye is seen to be almost round with the diameter from the optic nerve to the outer epithelium being slightly greater.

Th body epithelium is continued over the eye to form the outer cornea, the cells making up this layer being just as tall and in some cases taller than the cells in other parts of the surface epithelium. These cells, however, lack the pigment found in the cells of the general body epithelium. Surrounding the eye and outer end of the optic nerve, and continued for some distance along the optic nerve is a layer of connective tissue. This connective tissue layer is continuous as a thin layer beneath the outer cornea, appearing as a layer of closely irregular shaped cells with round nuclei.

The retina is crescent-shaped with the deepest part located in the center opposite the optic nerve. The retina is composed, as far as I can ascertain, of one type of cell. The retinal cells are very tall columnar cells which bear a brush of "hairs" or cilia-like processes on their outer end. The outer two-thirds of the cells is black because of the presence of numerous large round black pigment granules. The bases of the cells are drawn out into pointed ends which appear, structurally at least, to be continuous with the nerve fibers from the optic nerve. Toward the extreme outside of the retina are a few cells which do not bear the cilia-like processes. These may correspond to the supporting cells described for some gastropods (Prashad, 1925).

The edges of the retina are continued as a thin and almost structureless inner cornea, the cells of which do not have definite outlines and are devoid of pigment.

The cavity surrounded by the inner cornea and retina is filled by a well developed round pale yellowish lens. In sections it appears as a structureless round mass which does not take any of the common stains.

Excretory System

The renal organ is located to the right of and adjacent to the pericardium. It is divided into a larger posterior part which lies nearer to the pericardium and a smaller anterior part which is located on the right side of the whorl. The posterior renal organ is oblong in shape with faint lines or striations on its surface. In sections it appears spongy, very vascular gland made up of cells arranged in a somewhat crowded fashion. The organ is composed of many lamellae which apparently have fused together. This part of the renal organ is supplied almost entirely with venous blood by way of the afferent renal sinus and is drained by the efferent renal sinus directly into the auricle. The posterior renal organ is connected with the pericardial cavity by a very small opening on the one hand and with the chamber of the anterior renal organ on the other.

The anterior renal organ lies on the right side of the whorl and is much

smaller than the posterior part. Its surface presents a very definite coarse striated appearance due to the internal lamellar structure. This part of the organ has a spacious cavity into which hang a number of thin triangular lamellae. These lamellae are covered with a regular low cuboidal epithelium. In the center of each one is a large blood space separated from the epithelium by a very thin baseemnt membrane. The cavity of the organ opens into the tip of the pallial cavity to the right of the ctenidium by a small oval slit with thick ciliated "lips." The blood supply has been described in the section dealing with the blood system. From a survey of the literature it seems that there is not an abundance of definite information concerning the prosobranciate renal organ, especially as to its exact function, and it would be particularly desirable to reinvestigate the functions as well as to make a comparative histological study of the representative groups of fresh water prosobranchiates.

Reproductive System

The present study seems to demonstrate that the sexes in this species are separate. Over 720 specimens have been examined and in no case was any evidence of hermaphroditism found. As in many and perhaps all members of this family there are no external genitalia present in this species. The only external character present was described by Stimson (1864) and is best summed up by Baker (1928):

> The only apparent difference between the sexes appears to be the presence of a pit or sinus in the neck between the right tentacle and the operculigerous lobe, which is present in the female (with ova) and absent in the male (with sperm). . . A canal descends toward the base of the foot from this opening and become lost in the muscular tissue.

This character was present in the female studied and was indicative of the sex in every case. No other external sexual characters were discovered.

The position of the gonad is quite different from that of *Pleurocera acuta (Raf*inesque) briefly described and figured by Baker (1928). The gonad of *Pleurocera canaliculatum* (Say) is rather large and lies on the surface of the digestive gland, and reaching to and often forming the tip of the visceral hump. The testis, which is usually larger than the ovary, surrounds the digestive gland except for a strip on each side of the genital duct (Fig. 16). The testis has a lobulated appearance on the surface and is always light in color. It is composed of numerous branched tubular follicles. The sperm duct originates near the apex of the visceral mass and passes anteriorly with the visceral artery and a nerve from the visceral ganglion. At the region of the posterior end of the pallial cavity the closed genital duct ends and the genital tract continues forward as two opposed laminae with the two ventral edges joined to the floor of the pallial cavity on the right side at the angle formed by the floor and mantle. Posteriorly these folds are taller and swollen and are convoluted in an adult animal. The right fold is the taller and fits over the left to form an incomplete tube through which the genital products pass (Fig. 16). The genital folds are lined with ciliated columnar cells between which are a large number of gland cells. Covering the outside of the

folds are low columnar cells and an even greater number of gland cells than on the inside. Just beneath the surface epithelium is a thin layer of connective tissue and muscle fibers, and in the center of each fold is a large blood sinus which is in connection with the perirectal sinus. Passing across the lumen of the sinus are a number of very fine strands of muscle tissue.

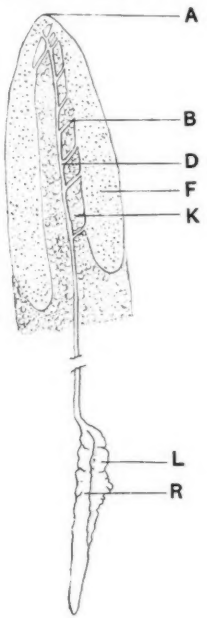


Fig. 16.
The genital duct and its relationship to the gonad seen as though uncoiled. A, apex of visceral mass; B, one of the small ducts which lead from the gonad to the main genital duct; F, gonad; K, digestive gland; L, left genital fold; R, right genital fold.

The spermatozoa are of two kinds: the hair-shaped sperm called the eupyrene (Meeves, 1903) and the worm-shaped or oligopyrene sperm. The latter are best called apyrene in this form. Neither of these, in this species, show any movement (Fig. 18). It is probable that here as in other similar cases, only the former type is capable of fertilizing the egg. Although these two types of sperm have interested zoologists since their discovery, little or nothing is known as to the function of the worm-shaped type (Siebold, 1836, Leydig, 1850, Baudelot, 1863, Simroth, 1891-1907, and Reinike, 1912, Woodward, 1935).

The eupyrene sperm consists of an elongate deeply staining head (Fig. 18, B) behind which is a long flagellum that gradually becomes smaller from the head to the tip. In front of the head is a hook-shaped structure which is as long as the head. It is to be noted that this sperm is very similar to that of *Goniobasis livescens correcta* (Brot.) described by Jewell (1931). The

terminal hook is either invisible or removed in most stained preparations, but it can readily be seen in fresh sperm.

The aprene sperm (Fig. 18, R) are more abundant in the early spring than in other seasons of the year. They are larger than the eupyrene and do not resemble them in the least. They are wider about the middle and taper gardually toward the ends which are blunt and rounded. No nucleus is visible but the whole structure is filled with coarse granules except for a narrow streak

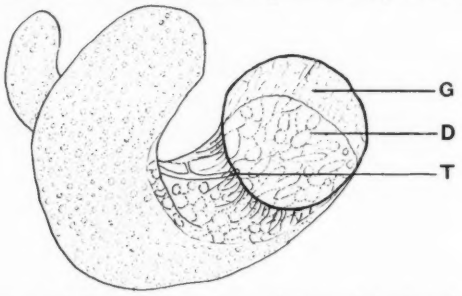


Fig. 17. Last wo whole of the visceral mass showing relationship of the gonad and the digestive gland. G, cut end of the gonad lying on the outer surface of the digestive gland (D); T, genital duct. x8.

in the center reaching the whole length, and a small area at one end. Occasionally large round chromatin granules are seen near the middle. Arising from the end where the clear area is located, is a tuft of from five to seven larg flagella. Jewell (1931) does not mention this type of sperm as occurring in *Goniobasis livescens*, however, Woodward (1935) has described their development in *Goniobasis laqueata* (Say) from Tennessee.

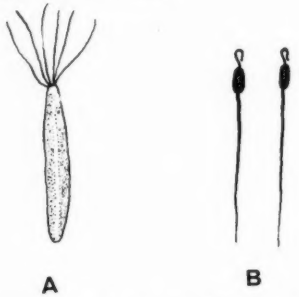


Fig. 18.
A. Apyrene spermatozoon.
B. Eupyrene spermatozoa.
x950.

The female reproductive system superficially is very similar to that of the male except the ovary is, in general, smaller and is reddish to brown in color rather than the light yellow of the testis. But during periods when they are not sexually active the gonads of both sexes shrink and tend to look a great deal alike externally. The ovary consists of branched tubular follicles. Ova

in various stages of growth can be seen attached to the germinal epithelium. The position and structure of the genital folds is about the same in the two sexes.

Neither copulation nor egg laying has been observed in this species, nor have egg masses been observed, except in a few cases. In fact, the eggs of only a very few species in the entire family have been recorded (Jewell, 1931, Van Cleave, 1933, Windsor, 1933, Woodward, 1934). There is a very definite need for further observation not only for a study of the minute anatomy of the gonads of members of this family but also of breeding activities and embroyology.

Summary

Approximately 720 animals, *Pleurocera canaliculatum undulatum* (Say), belonging to the family Peluroceridae, Order Ctenobranchiata, were dissected and the details of the anatomy investigated. The general anatomy was found to be similar to that of other members of this order. Of particular interest, however, is the discovery of a crystalline style and associated structures which have not before been described in this family. Likewise two types of spermatozoa have been identified: the eupyrene and the apyrene typs. This is one of the first records of spermatozoan dimorphism in the family Pleuroceridae. This study is intended as a basis for the investigation of the anatomy of other members of this family.

The writer wishes to thank Mr. Calvin Goodrich of the Museum of Zoology, University of Michigan, for identification of the animals used in this study.

REFERENCES

Baker, Frank C. 1928—The Fresh Water Mollusca of Wisconsin. Wisconsin Geological and Nat Hist. Survey, Pt. I, Bull. 70.

Baudelot, M. 1863—Recherches sur l'appareil générateur des mollusques gastropodes. Ann. Sci. Nat. Zool. **19**(4):135-222.

Bernard, F. 1890—Recherches sur les organes palleaux des gasteropodes Prosobranches. Ann. Sci. Nat. Zool. **9**(7):89-404.

Bouvier, E. L. 1887—Système nerveaux morphologie générale et classification des gastropodes Prosobranches Ann. Sci. Nat. Zool. **3**(7):1-510.

Copeland, M. 1918—The olfactory reactions and organs of the marine snails Alectrion obsoleta (Say) and Busycon canaliculatum (Linn.). J. Exp. Zool. **25**:177-227.

———1919—Locomotion in two species of the gastropod genus Alectron with observations on the behavior of the pedal cilia. Biol. Bull. **37**:126-138.

———1922—Ciliary and muscular locomotion in the gastropod genus Polinices. Biol. Bull. **42**:132-142.

Goodrich, Calvin. 1922—The anculosae of the Alabama River Drainage. Univ. of Mich. Pub. No. 7 (Mus. of Zool.)

Jewell, D. D. 1931—Observations on reproduction in the snail Goniobasis. The Nautilus **44**(4):115-119.

LACAZE-DUTHIERS, *H.* 1859—Mémoire sur la Pourpre. Ann. Sci. Nat. Zool. **12**(4):1-84.

———1872—Otocystes on capsules auditives des Mollusques (Gasteropodes). Arch. Zool. Exp. Gén. **1**:97-166.

LEYDIG, F. 1850—Über Paludina vivipara, Z. Wiss. Zool. **2**:125-97.

MAGRUDER, S. R. 1934—Notes on the life history of Pleurocera canaliculatum undulatum (Say). The Nautilus **48**(1):26-28.

———1935—Record of a crystalline style in two fresh water gastropods. The Nautilus **48**(3):100-102.

MEEVES, F. 1903—Über oligopyrene und apyrene Spermien und über ihre Entstehung nach Beobachtungen an Paludina und Pygaera. Arch. Mikr. Anat. **61**:1-84.

PRASHAD, B. 1925—Anatomy of the common Indian Apple-snail, Pila globosa. Memoirs Indian Museum **8**(3):91-152.

REINIKE, E. E. 1912—A preliminary account of the development of the apyrene spermatoza in Strombus and of the nurse cells in Littorina. Biol. Bull. **22**:319-327.

———1914—The development of the apyrene spermatozoa of Strombus bituberculatus. Carnegie Inst. of Washington. Pub. 183, **6**:197-238.

SIEBOLD, C. VON. 1836—Fernere Beobachtungen über die Spermatozoen der wirbellosen Tiere. 2. Die Spermatozoen der Paludina vivapara. Müller's Arch. Anat. Phys.; pp. 240-255.

SIMROTH, H. 1896-1907—Bronn's Klassen und Ordnungen des Thier-Reichs, Bd. **3**(2), Gastropoda, Prosobranchia.

SPENGEL, J. W. 1881—Die Geruchsorgane und das Nervensystem der Mollusken. Z. Wiss. Zool. **35**:333-383.

STIMSON, WM. 1864—On the structural characters of the so-called Melians of North America. Amer. J. Sci., 2nd ser. **38**:41-53.

TSCHACHOTIN, S. 1908—Die Statocysten der Heteropoden. Z. Wiss. Zool. **90**:343-422.

VAN CLEAVE, H. J. 1932—Studies on snails of the genus Pleurocera. I. The eggs and egg laying habits. The Nautilus **46**(1):29-34.

WINSOR, C. P. 1933—The eggs of Goniobasis virginica Gmelin and Anculosa carinata Bruguiere. J. Wash. Acad. Sci. **23**(1):24-36.

WOODWARD, T. M. 1934—Anatomy of the reproductive system of Goniobasis laqueata (Say). J. Tenn. Acad. Sci. **9**:243-258.

———1935—Spermic dimorphism in Goniobasis laqueata (Say). J. Morph. **57**(1):1-23.

DEPT. OF ZOOLOGY,
UNIVERSITY OF CINCINNATI,
CINCINNATI, OHIO

STUDIES ON THE LIFE HISTORY OF A SNAIL OF THE GENUS LIOPLAX *

HARLEY J. VAN CLEAVE AND RAY CHAMBERS

The family *Viviparidae* of the freshwater gastropods is, so far as known, confined to the northern hemisphere and is fairly well distributed over that portion of the earth (Baker, 1928). In North America the family is represented by four genera: *Viviparus, Campeloma, Tolutoma,* and *Lioplax.* In this country considerable attention has been directed to the taxonomy and nomenclature of the members of this family but very little has been known of the biology of individual species. In the laboratory of the senior author of this paper a program of studies on various aspects of the biology of *Viviparidae* has been in progress for several years. The life history of one species of *Viviparus* has been dealt with by Van Cleave and Lederer (1931) and several other papers have been completed awaiting publication. The present paper gives the results of a series of studies and observations on the life cycle of one variety of the genus *Lioplax.*

The subfamily *Lioplacinae* (Gill, 1871) Baker, 1926 is wholly an American group of more or less restricted distribution. The genus *Lioplax* is found in eastern United States and southern Canada, with exception of one species recorded from Eocene freshwater formation (Tejon beds) in California. Baker (1928: 48) has demonstrated that the recognition of this genus and its separation from *Campeloma* does not rest solely upon the superficial shell characters to which conchologists have limited their attention.

Aside from the contributions of Baker there is very little available material on the biology of any member of the genus *Lioplax* and Baker's observations are limited chiefly to a description of the morphology of the animal. Most of the references in the literature consist of records of the occurrence of members of the genus in streams of eastern and middle western United States. The present paper is a contribution to the life history of *Lioplax subcarinata occidentalis* in which particular attention has been directed to reproductive habits, length of life span, sex ratio, uterine development and rate of growth.

The writers wish to express indebtedness to the following individuals: Mr. Henry C. Markus for collecting materials; Mr. Frank C. Baker for tentative identification of the species and for numerous suggestions during the progress of the work; and to Dr. Henry A. Pilsbry for the identification of specimens and for making a name available for the unnamed variety of *Lioplax* which had long been recognized in the literature.

Lioplax has been under observation in this laboratory for a number of years. Frequent collections have been taken from the Wabash drainage and from the Mississippi and Illinois Rivers. All of these clearly represent a single variety as confirmed by determination of Pilsbry and of Baker. The subspecies *Lioplax subcarinata occidentalis* was given nomenclatorial status when Pilsbry

*Contributions from the Zoological Laboratory of the University of Illinois, No. 472.

(1935:143) applied the name to a concept which Baker had previously recognized in his "Mollusca of Wisconsin" where he stated (1928:52) "A distinct species of *Lioplax* occurs in Illinois, Indiana, and farther south . . . This form is figured by Binney (figs. 119, 120). Tryon, Haldeman, and Call each figures the western form of *Lioplax* and not the true *subcarinata* of Say." This newly christened form is the only representative of the genus which the writers have encountered in Illinois and in the adjacent states of Indiana and Iowa. This fact has greatly facilitated the present study since there has been no necessity of segregating mixed collections of closely related forms.

During the course of the present study field observations and collections were taken from the Wabash River at York, Illinois, the Illinois River above Peoria, Illinois, and the Mississippi River near Fairport, Iowa. While these rivers differ markedly in their characteristics, no attempt has been made to evaluate the specific influence of their differences upon the biology of *Lioplax*. It is worthy of mention that through central and southern Illinois large rivers have been the only ones in which *Lioplax* has been found though Pilsbry (1935:144) mentions that it 'is a common snail in Indiana, Illinois, and Iowa.' Of the three rivers mentioned above, the Wabash proved the most available for field observation and collections. Beginning with the summer of 1932 field studies were made at intervals of approximately one month until interrupted by a period of excessively high water from January to June of the following year. From time to time additional colections and field studies have been made which in the composite give information on *Lioplax subcarinata occidentalis* for all months of the year except April and May. During these months the streams under observation have experienced flood waters even in the years which have been marked by severe summer drought. Close association of *Lioplax* with specific types of river bottom renders quantitative collecting in high water impossible for the snails do not migrate to the new shore zone even when waters remain at flood stage over periods of several weeks.

In all of the collecting an effort has been put forth to secure quantitative samples. Turbidity of the water and burrowing habits of the snails did not permit of direct observation on *Lioplax* in its natural environment, hence samples were taken with a dip net. By going over the surface of a given bottom area several times approximately one inch of the silty mud was strained through the net giving a fair sample of the snail population. In all three of the stations selected for study other snails were associated with *Lioplax* but in varying combinations. From the Mississippi River at Fairport, several hundred specimens of *Campeloma* were associated with a small sample of twenty-six *Lioplax*. In the Illinois River above Peoria, *Campeloma* and two species of *Viviparus* were intimately associated with *Lioplax*. Mixed populations of *Campeloma*, *Lioplax*, and *Pleurocera* were always encountered in the same habitat in the Wabash River at York. Successive visits to the same stations yielded highly variable results. At one time the snails were concentrated into rather limited areas but on another visit they were widely scattered. Consequently, no fixed area could be established as a unit for securing a population sample. On one occasion 140 specimens of *Lioplax* were washed from ap-

proximately eight square feet of river bottom while a month earlier more than three times that area was covered in securing a comparable sample.

The modified right tentacle of the male, which serves as a copulatory organ, furnished a ready means of segregating the sexes. Field samples were preserved for further laboratory study and analysis which consisted chiefly in recording shell measurements and in the examination of the uterine contents of the females.

Graphs were prepared showing distribution of size groups based on shell height. Characteristic graphs are presented here as Figs. 1 to 5. Analysis of these distribution curves and observations on field and laboratory material throw light on a number of problems, chief of which have to do with relative size attainable by the two sexes in this species, differences in the length of the normal life span of the sexes, rate of growth, limitation of the parturition period, and many other details of the life history. Most of these problems will be discussed in the following section.

Analysis of Samples.—A large collection of 786 individuals, from the Mississippi River at Fairport, Iowa, taken on August 20, 1931 gave a very distinctive graph (Fig. 1) when a distribution curve based on height of the shells was prepared. In this and in all succeeding graphs (Figs. 1 to 5) the distribution curves are essentially bimodal. The writers interpret the two major modes as representing parent and offspring generations in a cycle involving but one reproductive period a year and with approximately two years as the limit of the life span. The differences in size and age attained by the two sexes and their influence on the distribution curves will be discussed in another section of this paper.

In the August sample (Fig. 1) the major modes fell at shell heights of 12 and 16 mm. with a confluent region between the two parts of the curve. As pointed out for another member of this same family of snails (Van Cleave and Lederer, 1932 on *Viviparus)* the members of the new generation grow at a much faster rate than those of the parent group. The fastest growing young individuals among the offspring soon equal or exceed in size the smallest of the parent individuals. This explains the confluence of the two distribution curves.

Studies on the uterine young and observations on the size of the smallest free living young taken from the streams, indicate that the young of *Lioplax subcarinata occidentalis* are approximately 2.5 mm. in shell height at birth. A few free living individuals in this size group were taken from the Wabash River at York, Illinois, in June and July, 1933, apparently at the close of a relativelly long parturition period. This last statement is supported by the fact that in no subsequent collection were individuals this small secured and further from the fact that in the June and July collections the mode for the main brood of the season had advanced to the group having shell height ranging from 6.5 to 7.4 mm.

From approximately 2.5 mm. at birth in late spring or early summer, the young individuals grow to a median height of approximately 7 mm. by late June or early July at which time the parent individuals have modes ranging

from 10.5 to 12.5 mm. This rate of increase is in direct keeping with that observed for *Viviparus contectoides* by Van Cleave and Lederer (1932). Members of this subspecies of *Lioplax* reach maximum size in the second fall or winter (about 23 mm.) but only females ever attain this age. Following the birth period in the second spring and early summer individuals of the maximum size groups entirely disappear from the population samples leaving no individuals over 16.5 mm. This period of elimination of the oldest individuals coincides with the period when the new generation is being added to the population, hence in the readjustment the bimodal nature of the population is but slightly disturbed.

As in other *Viviparidae* studied, there is wide range of variation in size of the embryonic young within the same uterus. This finds expression in variability in size of the young produced in the same brood and in extension of the parturition period over considerable length of time for the species. The shell of the adult snail is so translucent that the uterus and its contents are often distinguishable through it. The eggs within the uterus are usually hexagonal in surface view, due to their crowded condition. This observation seems to be directly correlated with the fact that the eggs and uterine young remain in relatively constant positions within the uterus and do not show the random mixing of various stages. This is in contrast to conditions encountered in the closely related genus *Campeloma* whose uterus is spacious and within it the eggs and young become irregularly dispersed.

Sexual dimorphism.—Interesting diversity of conditions of the sexes have been found in the *Viviparidae*. Separate sexes occur in the most of the species of *Viviparus* (Van Cleave and Lederer, 1932) though some are hermaphroditic (Alonte, 1930). In the genus *Campeloma* many of the species have separate sexes though unpublished observations give evidence of an anomalous condition in one species of this genus. In the present study on *Lioplax*, especial attention was directed to sexual dimorphism and to problems of differential limits to growth and age in males and females.

Segregation of the sexes revealed conditions of size dimorphism similar to those previously established for *Viviparus contectoides*. In the present study of *Lioplax subcarinata occidentalis* no male greater than 15.8 mm. shell height was discovered, though females were found in the same habitat reaching 23.3 mm. In the graphs (Figs. 1 to 5) the sharp limitation of males to the smaller of the two distinct size groups is strikingly consistent. The fact that females grow more rapidly than males of the same age is indicated by the distribution curves in Figs. 1 to 5, in all of which the curve representing the male portion of the population tends to have a mode distinctly below the mode of the general population of the same age group. Before these facts were ascertained it had been noticed that when field samples were segregated there appeared great diversity in the proportions of the sexes in different seasons of the year. In every sample studied, the females outnumbered the males but without any fixed ratio. This fact made the calculation of sex ratios practically meaningless until the data were further analyzed so as to compare the relative numbers in corresponding age groups.

Throughout the summer months, the collections usually contained less than

1.7 females to 1 male with considerable variability in individual samples. During the winter months, the incidence of females rose abruptly until in a November collection there were 3.72 females to 1 male and in a December sample there were 4.33 females to 1 male. The writers considered the possibility of sex reversal as a means of explaining this disparity in proportions of the sexes but the high degree of specialization of the male copulatory apparatus and complete lack of evidence of morphological changes in the bodily organization seem to preclude sex reversal from the possible explanations. Moreover, all of the evidence seems to indicate that in this species both sexes have definite limits to shell size and these seem to be intimately correlated with restrictions to the normal length of life.

Males of *Lioplax subcarinata occidentalis* tend to be smaller than females of the same age as mentioned in a preceding paragraph. This fact tends to complicate the calculation of relative numbers of the two sexes. In the region of the distribution curve where the two generations of females become confluent no means has been discovered for determining the age of the individual snails. Since females regularly surpass the males of the same age the upper limit of size in the male population gives only an approximate position for the limit of females of the same age. Taking this upper limit of size of the males as basis for calculating the limits of the one year group, there is direct evidence that males and females are equally represented in the population at birth and throughout the first year. Discrepancies in the sex ratios of samples are explainable wholly on the basis of elimination of males from the group more than one year of age.

The life cycle.—The available evidences seem to point to definite conclusions regarding the life cycle in members of the subspecies *Lioplax subcarinata occidentalis*. Males live normally to be approximately one year of age, go through a single breeding season and disappear before their offspring are born. Females normally live to an age of approximately two years, begin to bear eggs and young in their first year, and continue to produce young in their second year. Field collecting in the streams and study of the uterine young throughout the year give proof that but one generation is produced each year in the habitat under consideration. Some shelled embryos or eggs are present in the uterus of some females through most of the year. Females of samples taken in June contained eggs only, the young having apparently been liberated at an earlier date. By July females from the same station bore from four to nine shelled young and numerous eggs in each uterus. Shelled young continued to be present in the uteri from all subsequent collections throughout the summer, fall and winter and a few individuals taken on March 7, 1933 contained both eggs and shelled young. One female from this last named sample carried thirty-four fully shelled young and twelve developing eggs. The continued presence of shelled uterine young at all dates between July 26 and March 7, coupled with the fact that no small individuals of comparable size were found free in the river during this same period indicate that there is a single parturition period for this species and that the young are liberated only during the late spring and early summer. The establishing of this period as the one in which young are born, brings *Lioplax subcarinata occidentalis* into

close harmony with the reproductive habits of *Viviparus contectoides* and of *Campeloma rufum*.

The smallest free living young found in the streams were 2.7 mm. in shell height. The only collections in which individuals of this size were recorded were limited to the months of June and July but as previously stated no samples were available in the months of April and May because of periods of excessively high water. From September through March the gravid females carry shelled young many of which exceed 2 mm. in shell height. The foregoing facts supported by evidences of the growth rate of the young in the stream and the fact that most of the young have left the maternal uterus by June lead to the obvious conclusion that most of the young are liberated in a period of a few weeks in the months of May and June.

Summary

1. Periodic quantitative samples of *Lioplax subcarinata occidentalis* from the Wabash, Illinois, and Mississippi Rivers have been subjected to study over a period of years. Field observations and statistical analysis of samples have been combined to secure an understanding of the life history of this subspecies.

2. Graphs prepared to show distribution on shell height were regularly bimodal. Each mode represents a separate generation.

3. There is but one brood per year.

4. Males are smaller than females of the same age.

5. Males live to be approximately one year of age, attaining a maximum shell height of 15.8 mm. and going through a single breeding season.

6. Females live to be approximately two years of age, attaining a maximum shell height of 23.3 mm. and beginning to bear young in the first year.

7. Young snails vary considerably in size. They are approximately 2.5 mm. in height at birth and are liberated into the stream in late spring or early summer.

8. Young occur in the uterus of the females throughout the first year until early spring. The numbers increase progressively through the summer, fall and winter.

9. At one year of age the shell is 10.5 to 12.5 mm. in height.

10. Sex ratios are profoundly influenced by differential in length of life span for the two sexes.

11. A summer sample gave the ratio of 1.7 females to 1 male. The ratio increased until a December sample gave 4.33 females to 1 male.

REFERENCES

ALONTE, F. H. 1930—Biology of Vivipara angularis Mueller, a common fresh-water snail in Laguna de Bay. Philippine Agric. **19**(5):307-325.

BAKER, F. C. 1928—The Fresh Water Mollusca of Wisconsin. Part I. Gastropoda. Wisconsin Geol. and Nat. Hist. Survey, Bull. **70**.

CALL, R. E. 1886—The genus Campeloma, Rafinesque, with a revision of the species, recent and fossil. Bull. Washburn Coll. Lab. **1**:149-168.

PILSBRY, H. A. 1935—Lioplax subcarinata occidentalis, new subspecies. Nautilus **48**(4):143-144.

VAN CLEAVE, H. J. 1934—Length of life span as a factor in regulating populations. Ecology **15**(1):17-23.

VAN CLEAVE, H. J. AND L. G. LEDERER. 1932—Studies on the life cycle of the snail, Viviparus contectoides. Jour. Morphol. **53**(3):499-522.

EXPLANATION OF FIGURES

Graphs showing distribution of population samples of *Lioplax subcarinata occidentalis*. Each graph represents the percentage of individuals in the sample plotted against the height of shell. Divisions on the abscissa represent medians in increments of 1 mm. Thus 7 represent the total of those individuals having shell height from 6.5 to 7.4 mm.

Solid lines represents the entire population, broken lines indicate males.

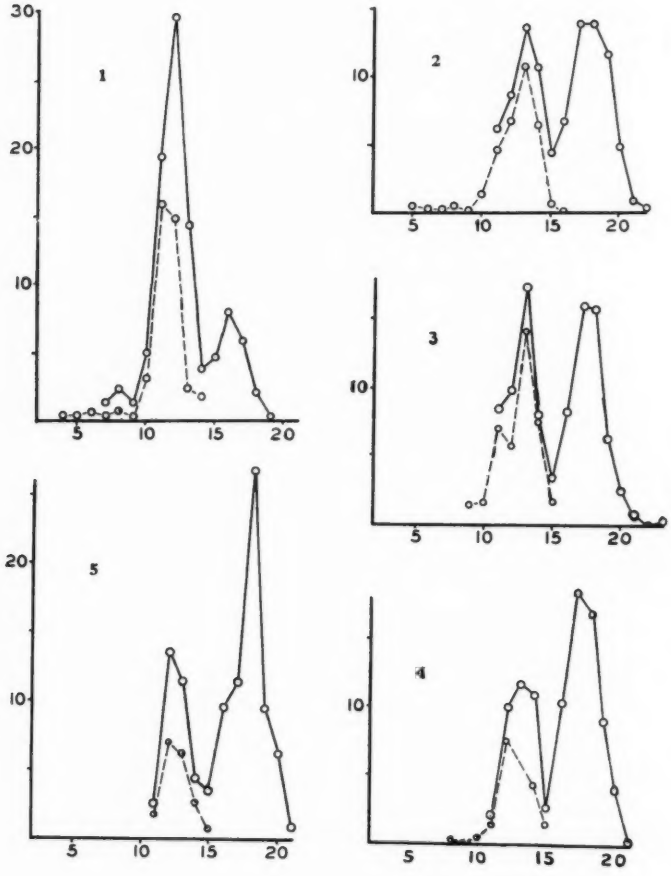
Fig. 1. A sample of 786 specimens of *Lioplax subcarinata occidentalis* from the Mississippi River at Fairport, Iowa, August 20, 1931.

Fig. 2. A sample of 932 specimens from the Wabash River at York, Illinois, September 19, 1932.

Fig. 3. A sample of 402 specimens from Wabash River, October 16, 1932.

Fig. 4. A sample of 189 specimens from Wabash River, November 27, 1932.

Fig. 5. A sample of 112 specimens from Wabash River, December 21, 1932.


1
2
3
4
5
30
20
10
5
10
15
20

NATRIX SIPEDON SIPEDON IN CENTRAL INDIANA

ITS INDIVIDUAL AND SEXUAL VARIATIONS

CHAPMAN GRANT

This paper embodies the results of an attempt to solve the problem of individual and secondary sexual variation in *Natrix sipedon sipedon*, a species that inhabits a wide area. It is believed that data from a large series of specimens from one locality is of value to students who wish to study the species in other parts of its range and makes geographical variation more easily apparent. To this end a series of sixty-five specimens was taken at the Grassy Fork Fish Hatchery in Morgan County, Indiana, in the spring of 1933. The hope of securing a larger series and making observations throughout the season was frustrated by my moving.

The field notes made while taking these specimens may serve as an introduction: The country around the fish hatchery consists of rolling limestone hills that produce a fair stand of hardwood on a thin soil; the bottoms are rich and cultivated. The hatchery comprises about fifty acres of spring and creek-fed ponds, varying in size from small to several acres in extent, and producing large numbers of goldfish. The snake population is probably constantly recruited from adjacent territory as the attendants kill large numbers.

The greatest loss of goldfish is from parasites and fungi, but some toll is taken by birds, frogs, turtles, game fiish and snakes. Stomach contents were checked to determine which vertebrates were the most destructive to the fish. Bull frogs, *Rana catesbeiana*, were found to have eaten goldfish. Garter snakes, *Thamnophis sirtalis sirtalis*, consumed about equal numbers of fish and frogs. *Natrix* had eaten fish only; the blue racer, *Coluber constrictor flaviventris*, devoured small mammals and small *Natrix*. Turtles were not taken, and only species seen were *Chelydra serpentina*, *Amyda* sp., and *Chrysemys marginata marginata;* the former probably eat goldfish. Kingfishers, grebes, and herons are scarce, but they do eat a few fish; the slaughter of these occasional visitors to save the few fish they consume seems unreasonable.

The hatchery was first visited on April 9, 1933. Attendants stated that but few snakes had been seen prior to that date. Nearly all *Natrix* seen were on the banks, and the caked mud on their scales probably still persisted from their subterranean hibernation. They were torpid, and hardly reacted when they were picked up. One specimen was lying at the bottom of a small stream.

A small *Natrix kirtlandii*, the only one of that species taken, was found under a chip of wood. It became rigid and flattened, looking like a dead roadside snake, a trick heretofore noted of this species. Female *Natrix* were extraordinarily fat; the ovaries contained from forty to sixty eggs about one cm. long interspersed with smaller eggs. No large *Natrix* were seen and the majority of smaller ones were males. *Thamnophis* was active, and two pairs were taken mating. Green frogs, *Rana clamitans*, and cricket frogs, *Acris gryllus*, were very numerous; bull frogs were scarce and leopard frogs, *Rana pipiens*, were not seen at all until later in the season.

April 16th. *Natrix* was very alert. About twenty-five were seen sunning on banks and in low bushes. No specimens were taken under boards. The sexes were about evenly represented, but no large specimens were seen. Green and cricket frogs appeared in great numbers. A snapping turtle, apparently just hatched, and a few painted turtles were seen.

April 23rd. Chilly, but *Natrix* was active. The specimens seen were very fat and the alimentary tracts empty, as on April 16th, except in the case of two large females which had each eaten one goldfish. There were no signs of mating.

April 30th. *Natrix* still very fat and but few contained food. They slip off banks into holes under water whence, with a little dexterity they may be extracted by hand. *Coluber* seen for the first time. In contrast to *Natrix* they were all very thin and had eaten snakes or mammals or both. One tried to escape by climbing into a tall bush. One was seen on a hillside apparently stalking a *Thamnophis*. *Coluber* was observed vibrating its tail among dry leaves, producing a sound which resembles that made by a rattler.

May 7th. Small *Natrix* were seen in numbers for the first time. One adult pair was found mating. The skin of *Natrix* apparently has great regenerative power as some specimens bore large scars made by spears of the hatchery attendants who seek to destroy them. The color pattern is regenerated but scales do not reappear on the scar tissue.

May 14th. *Natrix* was preparing to shed, as several were seen with eyes and bellies of a milk color which denotes the loosening of the skin. This was the earliest shedding noted. No specimens of *Natrix* had yet been found under boards, a favorite hiding place in other localities later in the season.

Summary on Observed Habits of Natrix

Natrix hibernates in banks adjoining feeding waters.

The males are the first to emerge early in April. They are very fat, sluggish and bear caked mud on their backs.

By the middle of April the sexes are equally numerous. They are alert but still very fat and have not yet started to feed or mate.

Toward the latter part of April they start to feed, the females more freely than the males.

Early in May the young of the previous year appear in numbers. The mature individuals start mating. By the middle of May shedding has become general.

Study of Squamation

Study of the upper head scutellation shows that the only variation found occurs in the oculars, labials and temporals. The arrangement of the temporals seem to be the sole sexual peculiarity. This variation is accomplished by the arrangement of the scales as is shown later, and is accounted for by the fact that the head of the female is larger in proportion than that of the male.

Oculars

Normally there is one preocular and three post-oculars on each side. The arrangement may be expressed by the formula, 1:3, 1:3,—the first figure representing the right side, the second the left. The preoculars are subject to little variation, there being only two specimens abnormal on both sides, and four abnormal on one side. Expressed in percentage, there are 6% abnormal preoculars, and 12% abnormal postoculars. Expressed in a table the details are:

Formula	1:3, 1:3	1:2, 1:3	1:3, 1:2	1:2, 1:2	2:3, 1:3	2:3, 2:3	2:4, 1:4
No. of Specimens	49	5	3	3	2	2	1

The only specimen which showed any correlation between abnormal oculars and other abnormalities was the specimen showing 2:4, 1:4. It also had additional labial scutes at the end of the series.

Labials

There are normally eight upper labials and ten lower ones. This may be expressed 8:10, 8:10 for the right and left sides respectively. In immature specimens the labials are easily counted at the corner of the mouth where the series end, but in older specimens it is sometimes not clear where the labials end and the body rows commence.

Only one specimen is abnormal in upper and lower labials on both sides. One upper jaw and five lower jaws are abnormal on both sides. Five upper jaws and nine lower jaws are abnormal on one side. This gives a percentage of normality of 75. In detail:

No. of Specimens	Formula	Sex	Specimen Number	Remarks
49	8:10, 8:10			25 ♂ and 15 ♀. Nine are juveniles, sex undetermined.
2	8:11, 8:10	Juv.	39b	A large scale is forced in between Nos. 7 and 8 lower left.
		♀	8	Third lower right labial is divided into two scales.
2	8:10, 8:11	♂	55	Third lower left labial divided into two scutes.
		♀	18	Scute added at end of lower left series.
3	8:11, 8:11	♀	83	Scute added at end of lower right and left series.
		♂	66	Scute added at end of lower right and left series.
		♀	31	Scute added at end of lower right and left series
1	8:10, 9:10	♀	56	Eighth upper left labial divided into two.
1	9:10, 8:10	♂	52	Second upper right labial divided into two.
1	9:11, 9:10	♂	50	Scute added at end of upper series on both sides. A very small scale between the upper adjacent angles of 9th and 10th lower right labials.
1	8:9, 8:10	♂	86	Lower 6, 7 and 8 labials apparently too large and no one seems to be double.
1	9:11, 9:11	♂	1	Second upper and third lower divided on each side. This is the most interesting case.
1	8:12, 9:12	♀	84	Third lower divided on each side. Scute added at end of upper left and lower right.
1	9:11, 8:10	♀	57	Scute added at end of upper and lower right series.
1	8:10, 8:9	♀	40	Second lower left labial missing. First is large.
1	7:10, 8:10	♀	33	Fourth or fifth upper right labial missing, but appears to have been excised and the adjacent scutes enlarged to fill in.

Temporals

The temporal scales show very little abnormality, but considerable variation of arrangement. The female is longer and disproportionately heavier than the male. A difference in size is usually correlated with enlargement of the scales, but a disproportionate enlargement is usually accompanied by additional scales or rows of scales, or by a different arrangement of scales. In one case the temporal scales occupy the angle between the upper labials and the parietals, and lie posteriorly to the postoculars. In this case, we invariably find one scute filling the point of the angle and this is ordinarily followed by three more scutes of about the same size. In the more bulbous-headed females, these three scales are usually arranged in a vertical row, each broadly in contact with the first temporal. The expression then is 1:3, 1:3 for right and left side respectively. The more narrow headed male usually has the three temporal scutes so adjusted that the central one is entirely displaced to the rear, coming broadly in contact with the first and third which now impinge. Or, the central scute is wedge shaped, having an anterior point which may or may

not reach the anterior temporal; or, the point of this wedge shaped scale is cut off into a small scale which touches all four of the temporals. The first of these three dispositions would be expressed, 1:2, 1:2. The second and third might be expressed in either way. There are exceptions to this secondary sexual index and some individuals show one arrangement on one side and another on the other.

Squamation of Body

The body of a snake is covered with alternately disposed scales. This arrangement results in the establishement of diagonal as well as longitudinal rows. The number of rows, their disposition and the place of their diminution are, to a certain extent, diagnostic. Therefore, a uniform method of counting is desirable. The best method of counting consists of zig-zagging across so as to finish at the opposite end of the gastrostege at which the count began. Normally a body count should be uneven because of the odd central row. An exception to this must mean that one of a pair of rows does not end opposite its mate.

Hypothetically, the simplest or ancestral snake would show close correlation between the number of teeth, the number of labials and the number of body rows. Differentiation of head scutes and constriction at the neck nearly hides all correlation in the present species, but a diagram shows the importance of stating at what point the first body count is made because of short rows on head and neck. Thus one observer might count 25-23-21 and another 27-25-23-21 on the same specimen.

Origin of Gastrosteges

The origin of the single row of wide gastrosteges, which extends across the belly of ground snakes, constitutes an interesting specialization. Modification must have arisen either from a form having a small-scaled belly as is approached by the Boidae or it must have developed by the widening of a single median row. The latter view is hardly tenable with the evidence at hand. The problem then is to determine how many rows were fused to form the gastrosteges in various species.

In *Natrix* we find the urosteges, preanal and geneials paired; a nick or re-entrant angle medially on the gastrosteges; and atavistic gastrosteges originating at one side and extending to the mid line only. Newman (1906, p. 107) points out that color pattern may indicate primitive scale rows in *Chelonians*. Color pattern leaves the midventral line clear in *Natrix;* evidence of a dividing line. Descent from an ancestral form with paired gastrosteges extending the full length of the body is plausible.

Newman (1906, p. 109) shows that circles or spots under one scute point to a former greater number of scutes. Thus the "V"s or half moons on the gastrosteges of *Natrix* may point to an earlier form that had more numerous rows. The number of labials may have a direct bearing on the original number of body rows. Thus the mental may be regarded as a pair of fused teminal gastrasteges. The "first lower labials" are clearly an intrusion of the second

pair of central gastrosteges between the mental and the "second" lower labial. By drawing these first lower labials down into place, the "second" now form an outer tier, or four-scale-wide ventrals.

The number of gastrosteges is a matter of interpretation as it is doubtful whether two students would make the same count. The chin of *Natrix* has two long geneials following the first and second infralabials. These are followed by two long postgeneials which diverge posteriorly. In the angle thus formed are found from 0 to 5 very small scales arranged tandem, in pairs, in threes or in any combination. The small scales are followed by from 2 to 6 scutes similarly arranged. Then commence the gastrosteges. However, it is impossible to determine which is the first gastrostege. In some cases, the first gastrastege seems to be well within the angle between the postgeneials; again, what might be counted as a gastrostege is paired with an elongated scute or is followed by two scutes or a deeply lobed scale or gastrostege.

It is generally understood that the preanal is not counted as a gastrostege, but frequently a half gastrostege is found anterior to the anal.

The numebr of gastrosteges in the sexes of *Natrix* varies only by one or two from a constant. The method of counting should always be indicated because the number of gastrosteges might indicate a sex-character though this point still lacks confirmation.

As a rule, specimens having the larger number of small scales have also the larger number of medium scutes preceding the gastrosteges. Disposition of scutes in 49 specimens:

No. of small scales	No. of specimens	No. of medium scutes	No. of specimens
0	2	2	27
1	10	3	9
2	23	4	6
3	10	5	3
4	2	6	4
5	2		

The gastrosteges of 33 males ranged from 135 to 144, averaging 139.3.

The gastrosteges of 24 females ranged from 135 to 142, averaging 138.9.

This means either that there is no difference, or that the series was too small to prove anything. The counts of juveniles are omitted because the sex could not be determined. Half gastrosteges anterior to anal were counted. The divided anal was not counted.

Urosteges

The urosteges of the above specimens, exclusive of broken tails in the males, ranged from 73 to 83 and averaged 76.8, for the females from 61 to 70 with an average of 65.3. This sexual difference of 23.5 is indicative of the difference in tail length and will be considered later.

Classification of Scale Rows

It is customary to consider the scales on the belly, or gastrosteges, apart from all the rest, which are grouped as dorsal and lateral rows. Another nomenclature calls all scale rows originating below the corner of the mouth the ventral, and those above the dorsal. Or the gastrosteges and the "first row," which is highly differentiated from those above is termed the ventrals; the rows originating with the eighth lower labial, or the second row, to and including all those rows originating with the temporals, are the lateral rows; those originating from the parietals, are called the dorsals; and the central row is designated as the median or spinal or central. The central row is the only one which appears to have originated as a single row. Newman (1906, p. 72, 92) believes that the central row of scutes originated as guards for the dorsal spines. Certainly there is no evidence of fusion of two rows.

The Central Row

The median, central or spinal row is sometimes missing where extra rows have been retained or "developed." At the head there are extra rows which serve to cover the bulbs of the jaws and give flexibility to the throat, where, a continuation of the wide gastrosteges would not permit the stretching necessary in swallowing. Other students have pointed out that various species have "developed" or retained keels or knobs in this area to rub while mating, producing sexual excitement. I believe that *Natrix* has retained additional scales for this purpose. However, it is remarkable that the central row should be missing at the two locations where extra rows are needed. It is possible that the central row has a direct relationship to ancestral skeletal modifications in these two areas and that these scutes are of the same or similar origin as those of the central row of scutes in Chelonians, Iguanidae, etc. Newman (1906, p. 101) believes that the interference of the carapace prevented the development of scutes in these areas in turtles. I believe that the absence or general reduction of spines in these areas was to accommodate vertical flexion in lizards, and that the absence of the central scale row in snakes is due to the same cause. Many snakes raise the fore part of the body but hold the head horizontal. All snakes that I have observed raise the tail while voiding.

Loss of Body Rows

A snake has the largest number of scale rows at the posterior part of the head. Several pairs of rows are dropped to accomplish the constriction of the neck. I have never seen a written rule according to which this happens. It appears, however, that the short rows start near the corner of the mouth and next the spinal. Occasionally a pair of rows is added for the enlargement of the body, and several pairs are lost as the body tapers towards the tail.

It has been found that *Thamnophis* drops pairs of rows symmetrically in the order 5, 6, 4, 7. The rule for *Lampropeltis* is 7, 6, 8, 5, 9, 4, being an alternate skipping, above, then below or vice versa. *Coluber constrictor* loses the fourth row only. *Natrix* usually drops rows in the order 5, 6, 4. The

writer has found that Alsophis drops 4, 9,—the ninth being the rows bordering the spinal, an arrangement fundamentally different from any of the above. These formulae disregard the short neck rows.

The method by which a row is dropped is interesting. *Thamnophis* loses a row by diminution in size of the scales, but *Natrix* and *Coluber* frequently drop a row without appreciable diminution in the size of the scales by ending against a larger scale. If it is difficult to determine which row is dropped, the following rule is usually correct: The row that ends has its terminal scale *nearer* the larger, following or "blocking" scale.

A dropped row frequently shows its influence several scales further back by the presence of a double-keeled scale, a very larg scale, a very small interpolated scale, or by reappearance as a row of varying length, sometimes only in the region anterior to the vent.

Scale rows were plotted principally from flat salted skins. The rows were traced, a thread was knotted in the last scale of a row, and the skins stored in bottles for reference.

Study of the charts shows that diminution of body size may be accomplished by dropping rows or by a decrease of the size of scales in a row. *Natrix* has a slender neck, but less than one third of the specimens examined drop rows anterior to the center of the body, and then invariably only one row on each side. Anterior diminution is accompanied by decrease of the size of scales instead of loss of rows because of the necessity for expansion in swallowing. Posterior diminution is associated with the loss of from two to four rows on each side as well as by scale diminution. No great distension is needed in the rear part of the body. The impulse of dropping many rows on the tail seems to start well forward on the body. The females lose, on an average fewer rows than the males, both anteriorly and posteriorly. When a row is dropped posteriorly it disappears about eight gastrosteges further back than in the males.

In this paper the "center" is determined by ascertaining the gastrostege at the middle of the short fifth row when this happens to stop both anteriorly and posteriorly. This is found to be about the 50th, counting from the head. The central gastrostege of the series is the 67th.

Graphically presented the diminution of scale rows of the specimens studied is as follows:

No. of Specimens	Males	No. of Specimens	Females
1.	19–21–23–21–19	1.	21–23–21–19
5.	21–23–21–19–17	1.	21–23–21–19–17
6.	23–21–19	6.	23–21–19
19.	23–21–19–17	9.	23–21–19–17
2.	23–25–23–21–19	6.	23–25–23–21–19
		1.	23–25–23–21–19–17
		1.	25–23–21–19

Diminution of the Tail

The loss of scale rows on the tail is interesting. The median or dorsal row which usually appears somewhat behind the head, stops several somites anterior to the vent, leaving the scales of adjacent rows not alternating, but side by side. By the time they have passed to the tail, there is an alternation, due probably to crowding. These two rows continue nearly to the tip of the tail.. It is interesting to note that the tip scales are urosteges. The lowest or No. 1 row on each side continues nearly to the tip. The intervening rows drop out. One row near the *center* of each side, No. 8, continues nearly to the tip. This is a diminution of an entirely different kind from that on the body, since 4 and 8 would be expected to drop out next after 5 and 7 respectively, instead of being nearly the last to disappear.

Use of the Tail

The scales on and near the tail are more prominently keeled than those on the larger part of the body. The tip of each scale is notched underneath to fit over the high keel of the succeeding scale. The fact that the keels are very high on and near the tail is not explainable on the ground of diminution of size of the cross section, for there is no parallel enlargement of keels at the nuchal constriction. Both sexes have the large scales, and these have little defensive or offensive value. It appears that the high ridges offer a better purchase on the water by offering more resistance and consequently a more effective vector. (Breder, 1926, p. 168). *N. compressicauda*, as its name implies, has met the problem in a more efficient way. Many good swimming snakes have comparatively smooth but proportionately longer tails.

Proportions

Tails have various uses. In snakes they may be prehensile; or they may be used for swimming, srawling, rattling and buzzing in which case no sexual differentiation in size is necessary, but they serve primarily for inclosing the hemipenis and musk glands of the male and only the musk glands of the female. The latter is true of *Natrix* and explains the necessary disparity in size of the tail in the sexes.

The most significant secondary sexual characters in *Natrix* are the proportions. The bulbous head of the female and attendant arrangement of the temporals has been mentioned. The greater number of urosteges in the male has been indicated. The proportionate lengths of the tail was studied in mature specimens with unbroken tails. The percentage of tail to body, snout to vent, ranges from 28 to 31% with an average of 29.3% in 22 females, and from 32 to 40% with an average of 35.5% in 30 males. This is a difference of 6.2%.

The bodies, snout to vent, of 21 females ranged from 41.5 to 93 cm.; tail 12.5 to 25.5; average total length, 92.4 cm. Thirty males ranged body, 42 to 66 and tails 16.5 to 21; total average length 71.2. Thus the females averaged 18.4 longer bodies and 2.8 longer tails. The males have tails proportionately 6.2% longer than females.

Pattern and Color

With the exception of some head markings the pattern seems to be permanent in the individual. The colors are not developed in the young, but show to best advantage in newly shed adults. The pattern of the back seems to grow indistinct as the snake approaches maturity. The head pattern of the young usually takes the form of dark centers of the plates and almost invariably there is a light spot or stripe immediately following the suture between the parietals, which constitutes the center of the first or nuchal saddle. These head markings tend to disappear with the growth of the snake.

The nuchal saddle is followed by other saddles reaching down to the gastrosteges. Between the ends of these saddles there are usually dark spots also reaching the gastrosteges. As this saddle and spot pattern progress backwards there is a migration of the ends of the saddles to coalesce with the spots and at the same time to migrate away from the center segment of the saddle, making a checker board pattern. In accomplishing this, there result intermediate W-shaped saddles. The variety of these changes is numerous. In some specimens the alternation again shifts to saddles and back again to checkerboard. In the young, these saddles and bars are black or dark brown without shades of red, the lighter centers being barely indicated.

The under side is usually unmarked anteriorly. Then arise two main rows of triangles with apices to the rear and two triangles per gastrostege. Progressing rearward the markings become heavier and blacker and frequently assume some regularity. The two gastrosteges bearing the black ends of the side bars, bear in addition two small triangles, whereas the next two, being free from influence of the side bars, bear two large semicircles. In the young, the triangles and semicircles are usually black, sometimes with gray centers or an indication of the red which is to develop later. In transitional places the pattern of the back grades all the way from the spots seem on *N. kirtlandi* to the checkerboard found on *N. rhombifera*. There is no confusion, merely a beautiful example of the derivation of patterns. The present form seems to be in the process of transition.

The number of dorsal blotches or saddles is more or less specific. In this group of specimens, the saddles varied from 27 to 34 with an average of 31. The nuchal saddles which do not alternate with the lateral blotches varied from 0 to 7 with an average of 3.2.

Summary on Secondary Sexual Differences in Natrix

The female is large and heavy bodied, averaging 34% longer than the male. Her tail is short, being about 30% of body length.

The smaller more slender tail of the male averages 5% longer than tails of females, and is about 36% of the length of the body.

The female usually has temporals 1:3, the male 1:2.

The male averages 76 urosteges; the female only 64.

The female usually drops the fifth long row opposite the 78th gastrostege; the male drops the fifth long row opposite the 71st.

Anterior reduction of scale rows is uncommon; one-third of the females and one-fifth of the males reduce. The anterior reduction seldom exceeds one pair of rows. The posterior reduction is two or three pairs and rarely four pairs of rows.

The female frequently has a maximum of 25 rows, usually reducing to 19.

The male usually has a maximum of 23 rows, usually reducing to 17.

REFERENCES

BREDER, C. M. 1934—The locomotion of fishes. Zoologica. N. Y. Z. S. **4**(5).

CONANT, ROGER. 1934—The Red Bellied Water Snake in Ohio. Ohio J. Sci. **34**:

HAY, O. P. 1892—The Batrachians and Reptiles of the State of Indiana. 17th Report, Ind. Dept. Geol. and Nat Resources.

NEWMAN, H. H. 1906—The significance of scute and plate "abnormalities" in Chelonia. U. of Chicago Biol. Bull. **10**(2/3).

SAN DIEGO, CALIFORNIA.

EGGS AND YOUNG OF THE PILOT BLACK SNAKE AND THE FOX SNAKE

FRANCIS HARPER

About September 5 or 6, 1933, a set of 13 eggs of the Pilot Black Snake (*Elaphe obsoleta obsoleta* (Say)) was collected by Paul Lewis in Indiana County, Pennsylvania, about midway between Plumville and Home Station. "They were found in the manure shed next to the stone wall of the barn," writes Mr. Lewis, "and were buried pretty deep. . . . I opened two of the eggs myself and was very much surprised at the size of the snakes, as they were at least a foot long and as thick as a lead pencil and were full of fight when the eggs were opened."

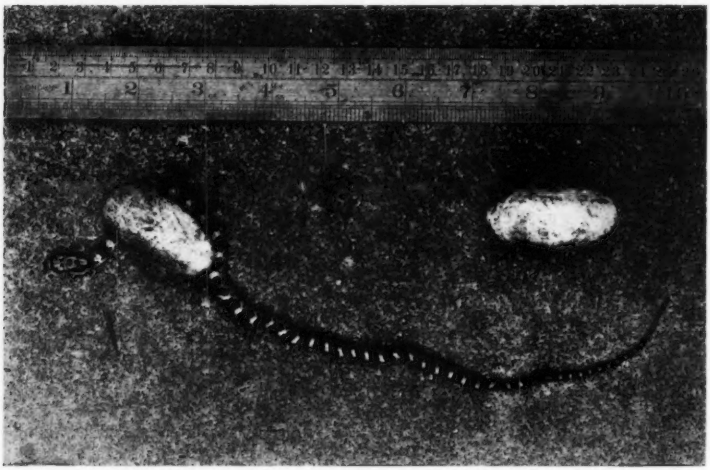


Fig. 1. *Elaphe obsoleta obsoleta*, about 11½ inches in length, at age of 1-3 days, with two hatched eggs. Sept. 16, 1933.

Through the interest of R. W. Wehrle, of Indiana, Pa., eight eggs of this set were mailed to Henry W. Fowler, of the Academy of Natural Sciences of Philadelphia, who generously turned them over to me for study.

By the time of their arrival in Philadelphia, on September 13, one of the eggs had hatched. By the morning of September 15 another egg had hatched, and from a third egg a head was projecting about half an inch. By evening this head had extended more than an inch beyond the shell. Meanwhile the two fully emerged youngsters were observed by my wife to engage in a fight; one seized the other by the neck, but retained its hold for only a second or two. By the morning of September 16 the third snake was out of its shell.

From September 15 to 21 the eggs were kept in a terrarium among bits of damp wood. On the latter date I opened two of the remaining five eggs and preserved the fully formed but lifeless embryos within. A considerable amount of yolk still remained in the shells. The other three eggs were discarded, at least one of them having become moldy on the outside.

The eggs, discolored by the matter in which they had been laid, were dirty white. Each of the three young snakes had emerged through a narrow slit (averaging about 10 mm. in length) between the middle and the end of its tough, leathery eggshell. All the eggs were dented (the unhatched ones more deeply than the hatched), rendering it impossible to secure altogether normal measurements. The three hatched eggs measured: 48.5X24, 47X23, and 42X27 mm. The five unhatched eggs measured: 48X24.5, 44.5X25.5, 44X26, 41.5X26.5, and 41.5X26.

On September 16 the three young snakes, at ages varying from about one to three days, were roughly measured, exact results not being obtainable owing to their liveliness. One was approximately 11½ inches (292 mm.), the other two approximately 12½ inches (317 mm.). One of these, after being fixed on September 26, measured 321 mm. The two embryos preserved on September 21 measured 288 and 301 mm.

An effort was made to keep the three young snakes alive for a few days in Swarthmore, Pa. One escaped, however, and another disappeared, possibly through cannibalism on the part of its fellow. The lone survivor was preserved on September 26. Meanwhile no molt had been observed.

Proper identification was not made until the young ones had been carefully examined for structural characters. Up to that time they had been looked upon as a peculiar color phase of *Lampropeltis tricngulum triangulum*. The statement that the young of *Elaphe o. obsoleta* are like *E. o. confinis* is far from a complete or satisfactory description.

A minute egg-tooth at the tip of the premaxillary is apparent in the two embryos, while that of the young snake preserved on September 26 has been shed or otherwise lost. In these three specimens there are 36-37 median dorsal blotches anterior to the vent, and 15-17 beyond. The average distance between blotches is about equivalent to twice the length of a scale. The accompanying photograph (Fig. 1) indicates their shapes better than words can. The first blotch is Y-shaped and reaches the parietals. There are two irregularly alternating series of smaller blotches on each side below the large median series; the lower of these two series is chiefly on the ventrals. Nearer the middle of the whitish ventrals, on each side, is an additional series of small quadrate blotches. There are a few small blotches on the frontal and parietals. All the above-mentioned blotches are slaty black. A band of the same color extends from eye to eye across the posterior portion of the prefrontals, and continues behind the eye obliquely to the angle of the mouth. The sutures between the first 6-7 supralabials and between the first 8-9 ralabials are streaked with blackish. The ground color of the dorsum is grayish white, each scale being marked with a tiny dusky spot. The median rows of dorsal scales are faintly keeled.

The appended bibliography contains references to the comparatively meager

authentic or original literature on the eggs and young of this snake (Hay, 1892a, pp. 395-396; Surface, 1906, pp. 159-160; Ditmars, 1907, p. 306; Hurter, 1911, p. 179; Netting, 1927; Corrington, 1929, p. 73; Myers, 1930, p. 102; Boyer and Heinze, 1934, p. 196). All of these accounts, as well as the present one, are incomplete. One of the important points remaining to be determined is the incubation period under natural conditions. The natural places in which the eggs are recorded as being laid include "loose earth or damp sawdust" (Surface, 1906, p. 159) and "a hollow stump" (Stejneger, in Hay, 1892a, p. 396). Since the eggs reported by Stejneger were collected near the Potomac River "early in April," it would appear that the "fully developed young" contained therein had hibernated within the eggs. Surface's statement (1906, pp. 159-160) that the eggs are laid "during the latter part of August or early part of September" and hatch "during the first and second weeks of September" scarcely makes allowance for a sufficient incubation period. His figure (1906, pl. 25) is possibly the only one of the young published hitherto.

The present seems an opportune occasion for correcting a long-standing error in the literature that involves another species of *Elaphe*. Hay (1892a, p. 396; 1892b, p. 119; 1892c, p. 518) records some eggs of the "house snake" (*Ophibolus doliatus triangulus*) as found "in midsummer . . . in a pile of stable manure" in Bureau County, Illinois, and gives their catalogue number as U. S. N. M. 17955. His measurements of the eggs (2 inches long and nearly 1¼ inches in the short diameter) and of an embryo within one of them (10¾ inches) considerably exceed those given by Surface (1906, p. 179), Ditmars (1907, p. 345), and Blanchard (1921, p. 194) for the eggs or young of *Lampropeltis triangulum triangulum*, as this snake is currently known. Nevertheless, Hay's record is accepted without question by Cope (1900, p. 886), Surface, and Blanchard. On the other hand, Ruthven, (1912, p. 92) refers the record to *"Elaphe obsoletus,"* without, however, making any comment as to misidentification on Hay's part.

In an effort to find a solution of this puzzling case, I wrote to Dr. Doris M. Cochran, of the U. S. National Museum, who very kindly sent me for examination the embryo and two eggs of U. S. N. M. 17955. At the same time Dr. Cochran informed me that the identification of these specimens had been corrected by Dr. Leonhard Stejneger sometime prior to 1919, and that they are now listed under *Elaphe vulpina* (Baird and Girard) in the card index of the U. S. National Museum. So far as I am aware, however, this correction has not appeared in print up to the present time.

Although the original embryo described by Hay is no longer in the best condition, there can be no doubt as to the correctness of Dr. Stejneger's determination of it as *Elaphe vulpina*. Its present length is approximately 258 mm. Though much faded, it still shows the characteristic color pattern of the species. It has about 58 dorsal blotches (41 of them anterior to the vent). (Blanchard's statement (1925, p. 14) of 31-38 dorsal blotches in this species applies to the body minus tail.) The first of these blotches is divided longitudinally into two. There is a band across the posterior part of the prefrontals, and an oblique band from the eye to the angle of the

mouth. There are about 200 ventral plates. A minute egg-tooth is present.

Another embryo, whose head I exposed by opening one of the two eggs (now about 42 x 28 mm.), is in much better condition, and its color pattern is much more clearly preserved. A number of small blotches appear on the frontal and parietals. The sutures between the anterior supralabials and infralabials are streaked with a light brownish color like that of the dorsal blotches. There are 8 supralabials and about 10 infralabials. A minute and ineffectual-looking egg-tooth appears at the tip of the premaxillary. There is a slight suggestion of keels on the median rows of dorsal scales.

The retention by *Elaphe vulpina* of its embryonic color pattern into adult life contrasts with the striking change in *E. o. obsoleta* from the blotched pattern of infancy to the nearly uniform dorsal coloration of the adult.

I am much indebted to Dr. Frank N. Blanchard for criticism of the manuscript.

REFERENCES

BLANCHARD, F. N. 1921—A revision of the king snakes: genus *Lampropeltis*. U. S. Nat. Mus. Bull. **114**: vi + 260, 78 fig.

———1925—A key to the snakes of the United States, Canada and Lower California. Papers Michigan Acad. Sci., Arts and Letters **4**(2):xiii+65, 78 fig.

BOYER, DOROTHY A., AND A. A. HEINZE. 1934—An annotated list of the amphibians and reptiles of Jefferson County, Missouri. Trans. Acad. Sci. St. Louis **28**(3/4):185-200.

COPE, E. D. 1900—The crocodilians, lizards, and snakes of North America. Ann. Rept. U. S. Nat. Mus. **1898**:153-1294, 36 pl., 347 figs.

CORRINGTON, J. D. 1929—Herpetology of the Columbia, South Carolina, region. Copeia **172**:58-83.

DITMARS, R. L. 1907—The reptile book. New York: xxxii+472, 136 pl.

HAY, O. P. 1892a—On the breeding habits, eggs, and young of certain snakes. Proc. U. S. Nat. Mus. 1892, **15**(art. 909):385-397.

———1892b—On the breeding habits, eggs, and young of certain snakes. Proc. Indiana Acad. Sci. **1891**:106-120. (This paper, practically identical with the preceding, is apparently of later date. 1892a was isssued Sept. 19, 1892; 1892b was received at the Academy of Natural Sciences of Philadelphia on Jan. 31, 1893.)

———1892c—The batrachians and reptiles of the State of Indiana. Indiana Dept. Geol. and Nat. Resources, 17th Ann. Rept. 1891:409-609, 3 pl.

HURTER, JULIUS, SR. 1911—Herpetology of Missouri. Trans. Acad. Sci. St. Louis **20**:59-274, 7 pl.

MYERS, G. S. 1930—Amphibians and reptiles observed in the Palisades Interstate Park, New York and New Jersey. Copeia **173**:99-103.

NETTING, M. G. 1927—A note on the egg-laying of *Elaphe obsoleta obsoleta* (Say). Copeia **162**:29-30.

RUTHVEN, A. G. 1912—The reptiles of Michigan. Michigan Geol. and Biol. Survey **10**(biol. ser. 3):63-166, illus.

SURFACE, H. A. 1906—The serpents of Pennsylvania. Monthly Bull. Div. Zool., Pen. Dept. Agric. **4**(4/5):113-202, 29 pl.,, 20 fig.

SWARTHMORE, PA.

BIRDS OF DALLAS COUNTY, TEXAS

CLAUDE KELLEY

For many years a number of people in the Dallas vicinity have been interested in bird study. Considerable time has been spent in the field by these individuals and several are working toward the completion of a usable check-list for this area.

The Dallas region is not on one of the main routes of bird migration. However, during the past six years of observation, it has been the writer's experience that most of our common migratory birds are seen in this section. A rolling prairie with scattered woods, small streams, several ponds, and one large artificial lake, (White Rock), characterizes this region. Since the majority of the observations cited in this paper were made in the White Rock area it seems apropos to describe briefly this vicinity. The lake originally covered an area of approximately 1600 acres, but due to the inevitable silting and several seasons of drought the surface has been reduced approximately one-tenth. The northern and part of the eastern boundary of the lake is marshy. Such plants as *Typha, Scirpus, Dianthera,* and *Salix* in the marshes provide excellent foraging and nesting places for water birds. Along the small streams that feed the lake are timbered areas that furnish shelter and provide food for migrants and residents.

The dates given for the migratory birds are for the spring and autumn migrations. In as much as this list contains the record of only one observer some of the less common species have been recorded only a few times and in some instances only once. All of the observations in this paper are sight records.

The terminology and arrangement used conforms to the "Fourth Edition of the American Ornithologist Union Check List." By comparing the A. O. U. Check List, Chapman's "Handbook of Birds of Eastern North America," Strecker's "Birds of Texas," and Simmons' "Birds of the Austin Region," there seems to be a probable total of four hundred species of birds in this region. This list contains two hundred and fifteen.

COLYMBIFORMES

Colymbidae—Grebes

Æchmophorus occidentalis (Lawrence)—Western Grebe. An uncommon winter resident.

Podilymbus podiceps podiceps (Linnaeus)—Pied-billed Grebe. Abundant winter resident, and fairly common in summer.

PELECANIFORMES

Phalacrocoracidae—Cormorants

Phalacrocorax auritus auritus (Lesson) — Double-crested Cormorant. Found once in the autumn of 1934.

Phalacrocorax olivaceus mexicanus (Brandt)—Mexican Cormorant. First observed on July 4, 1932. One has been at White Rock from Nov. 8, 1934 until late spring of 1935.

Ciconiiformes

Ardeidae—Herons and Bitterns

Ardea herodias herodias (Linnaeus)—Great Blue Heron. Seen ordinarily throughout the year.

Casmerodius albus egretta (Gmelin)—American Egret. A summer resident; one unusual record—Jan. 17, 1932.

Hydranassa tricolor ruficollis (Gosse)—Louisiana Heron. Fairly common summer resident; commonest in August and September.

Florida caerulea caerulea (Linnaeus)—Little Blue Heron. Rather uncommon resident.

Butorides virescens virescens (Linnaeus)—Eastern Green Heron. Uncommon summer resident.

Nycticorax nycticorax hoactli (Gmelin)—Black Crowned Night Heron. Fifty were at White Rock on Jan. 17, 1935 and were reported again on April 28.

Nyctanassa violacea violacea (Linnaeus)—Yellow-crowned Night Heron. A pair nested in a dead tree north of White Rock in the spring of 1933. The eggs were laid about April 30. Since then a number have been reported.

Botaurus lentiginosus (Montagu)—American Bittern. Fairly common in spring and summer; rare in winter.

Anseriformes

Anatidae—Ducks and Geese

Branta canadensis canadensis (Linnaeus)—Canada Goose. Common migrant.

Branta canadensis hutchinsi (Richardson)—Hutchins's Goose. Observed only once—Nov. 8, 1934.

Anas platyrhynchos platyrhynchos (Linnaeus)—Common Mallard. Common migrant and winter resident.

Anas rubripes tristis (Brewster)—Black Duck. Unusual winter resident.

Chalelasmus streperus (Linnaeus)—Gadwall. A few scattered fall records except for a flock that wintered from Nov. 1-June 1.

Mareca americana (Gmelin)—Baldpate. Common winter resident; Sept. 29-May 10.

Dafila acuta tzitzihoa (Vieillot)—Pintail. Common migrant and winter resident.

Nettion carolinense (Gmelin)—Green-winged Teal. Rather uncommon winter resident.

Querquedula discors (Linnaeus)—Blue-winged Teal. Common winter resident; Oct. 1-May 7.

Querquedula cyanoptera (Vieillot)—Cinnamon Teal. A large flock has been in this region throughout the winter of 1934-5.

Spatula clypeata (Linnaeus)—Shoveller. Common winter resident; Nov. 1-May 5.

Nyroca americana (Eyton)—Redhead. Fairly common; Oct. 28-May 12.

Nyroca collaris (Donovan)—Ring-necked Duck. Observed Nov. 23, 1928 and Jan. 10, 1935.

Nyroca valisineria (Wilson)—Canvasback. Uncommon winter resident, but a common migrant.

Nyroca marila (Linnaeus)—Greater Scaup. Very uncommon winter resident; Oct. 28-April 1.

Nyroca affinis (Eyton)—Lesser Scaup. Common winter resident; October 28-April 21.

Glaucionetta clangula americana (Bonaparte)—Golden-eye. Observed Oct. 28, 1928 and again throughout October, 1934.

Charitonetta albeola (Linnaeus)—Buffle-head. First seen in January, 1935.

Clangula hyemalis (Linnaeus)—Old Squaw. One record—May 12, 1935 at Bachman's Lake.

Erismatura jamaicensis rubida (Wilson)—Ruddy Duck. One at White Rock during the spring of 1935.

Falconiformes

Cathartidae—Vultures

Cathartes aura septentrionalis (Wied)—Turkey Vulture. The common vulture of this region.

Coragyps atratus atratus (Meyer)—Black Vulture. Much less common than the preceding.

Accipitriidae—Hawks and Eagles

Accipiter velox velox (Wilson)—Sharp-shinned Hawk. A few winter but no summer records are available.

Accipiter cooperi (Bonaparte)—Cooper's Hawk. Uncommon in winter; one summer record.

Buteo borealis borealis (Gmelin)—Red-tailed Hawk. Migrant and winter resident.

Buteo borealis krideri (Hoopes)—Krider's Hawk. Fairly common winter resident.

Buteo borealis harlani (Audubon)—Harlan's Hawk. Uncommon as resident; fairly common in winter and fall.

Buteo lineatus lineatus (Gmelin)—Red-shouldered Hawk. Fairly common all the year.

Buteo platypterus platypterus (Vieillot)—Broad-winged Hawk. Seen twice in the same locality; Jan. 29, and Aug. 28, 1933.

Buteo swainsoni (Bonaparte)—Swainson's Hawk. An uncommon hawk that has been seen since October, 1934.

Circus hudsonius (Linnaeus)—Marsh Hawk. Very common winter resident.

Pandion haliaetus carolinensis (Gmelin)—Osprey. One at White Rock April 25-May 10, 1935.

Falconidae—Falcons

Falco sparverius sparverius (Linnaeus)—Sparrow Hawk. Very common winter resident.

GALLIFORMES

Perdicidae—Quails

Colinus virginianus virginianus (Linnaeus)—Eastern Bob-white. A permanent resident.

GRUIFORMES

Rallidae—Coots and Rails

Porzana carolina (Linnaeus)—Sora. One pair at White Rock, July 4, 1935.

Gallinula chloropus cachinnans (Bangs)—Florida Gallinule. One record—May 5, 1935.

Fulica americana americana (Gmelin)—Coot. Common winter resident and fairly uncommon summer resident.

CHARADRIIFORMES

Charadriidae—Plovers

Oxyechus vociferus vociferus (Linnaeus)—Killdeer. Common resident.

Scolopacidae—Woodcock, Snipe, and Sandpipers

Philohela minor (Gmelin)—American Woodcock. Observed March 16, 1930 in a residential section along Turtle Creek.

Capella delicata (Ord)—Wilson's Snipe.—An uncommon winter resident in the marshes at White Rock.

Bartramia longicauda (Bechstein)—Upland Plover. About one hundred north of Dallas on April 15, 1933.

Actitis macularia (Linnaeus)—Spotted Sandpiper. Fairly common migrant and summer resident.

Tringa solitaria solitaria (Wilson)—Solitary Sandpiper. A summer resident and migrant. Common in October.

Catoptrophorus semipalmatus inornatus (Brewster)—Western Willet. Four were observed on May 16, 1935.

Totanus melanoleucus (Gmelin)—Greater Yellow-legs. Fifty wintered at White Rock; Oct. 28, 1929-May 30, 1930.

Totanus flavipes (Gmelin)—Lesser Yellow-legs. Common migrant; Oct. 18-Nov. 30; April 1-30.

Pisobia fuscicollis (Vieillot)—White Rumped Sandpiper. A flock of about twenty were seen at White Rock—May 21, 1933.

Pisobia bairdi (Coues)—Baird's Sandpiper. Only recorded once—Oct. 14, 1934.

Limnodromus griseus griseus (Gmelin)—Dowitcher. Seen at Barchman's Dam from Oct. 14-Nov. 1, 1934.

Crocethia alba (Pallas)—Sanderling. Aug. 31, 1933 and Nov. 8, 1934.

Laridae—Gulls and Terns

Larus argentatus smithsonianus (Coues)—Herring Gull. Often winters on White Rock; common summer resident.

Larus delawarensis (Ord)—Ring-billed Gull. Fairly common.

Larus atricilla (Linnaeus)—Laughing Gull. Observed May 11, 1931 following a plow in company with some Blackbirds and a Black Tern.

Larus pipixcan (Wagler)—Franklin's Gull. Observed from May 6-Nov. 2.

Larus philadelphia (Ord)—Bonaparte's Gull. Three of these Gulls on White Rock—Dec. 28, 1932.

Sterna forsteri (Nuttall)—Forsters' Tern. White Rock—Oct. 11, 1934.

Sterna hirundo hirundo (Linnaeus)—Common Tern. Has been observed during spring and fall of 1934.

Sterna fuscata fuscata (Linnaeus)—Sooty Tern. An accidental visitor—Aug. 29, 1932. The bird was exhausted and barely able to fly. When approached it flew weakly over some reeds and dropped into them.

Sterna antillarum antillarum (Lesson)—Least Tern. First seen during May 1935.

Chlidonias nigra surinamensis (Gmelin)—Black Tern. Two occurrences—May 11, 1932 and May 15, 1933.

COLUMBIFORMES

Columbidae—Doves

Zenaidura macroura carolinensis (Linnaeus)—Mourning Dove. Hunting has reduced the flocks until we now have but few doves.

CUCULIFORMES

Cuculidae—Cuckoos and Roadrunners

Coccyzus americanus americanus (Linnaeus)—Yellow-billed Cuckoo. Fairly common; April 1-Oct. 28.

Coccyzus erythropthalmus (Wilson)—Black-billed Cuckoo. Observed only once—April 13, 1929.

Geococcyx californianus (Lesson)—Road-runner. Permanent resident. Dallas seems to be on the very eastern edge of the Chapparal's range.

STRIGIFORMES

Tytonidae—Barn Owls

Tyto alba pratincola (Bonaparte)—Barn Owl. Observed only twice—Mar. 19, 1930 and Nov. 8, 1934.

Strigidae—American Owls

Otus asio hasbroucki (Ridgway)—Screech Owl. An uncommon resident.

Speotyto cunicularia hypugaea (Bonaparte)—Western Burrowing Owl. One was observed at the entrance to a burrow on Feb. 10, 1935.

Strix varia varia (Barton)—Barred Owl. Winter resident.

Strix varia helveola (Bangs)—Texas Barred Owl. Permanent resident.

Asio wilsonianus (Lesson)—Long-eared Owl. During the last few years there have been eight of these birds wintering among the cedars on the east side of White Rock.

Asio flammeus flammeus (Pontoppidan)—Short-eared Owl. Found one on Dec. 28, 1932. About fifty wintered at White Rock in 1934-35.

CAPRIMULGIDAE—Goatsuckers

Antrostomus vociferus vociferus (Wilson)—Whip-poor-will. Observed only once—Oct. 14, 1934.

Chordeiles minor minor (Forster)—Eastern Nighthawk. Very common migrant and summer resident—April 20-Oct. 31.

MICROPODIFORMES

Micropodidae—Swifts

Chaetura pelagica (Linnaeus)—Chimney Swift. Common migrant and summer resident; Mar. 23-Sept. 30.

Trochilidae—Hummingbirds

Archilochus colubris (Linnaeus)—Ruby-throated Hummingbird. Once reported on Feb. 28. Usually nearer Mar. 23-Oct. 21.

Archilochus alexandri (Bourcier and Mulsant)—Black-chinned Hummingbird. Summer resident arriving about April 2.

CORACIIFORMES

Alcedinidae—Kingfishers

Megaceryle alcyon alcyon (Linnaeus)—Eastern Belted Kingfisher. Common permanent resident.

PICIFORMES

Picidae—Woodpeckers

Colaptes auratus auratus (Linnaeus)—Flicker. The commonest of our woodpeckers. Very few breed here.

Colaptes cafer collaris (Vigors)—Red-shafted Flicker. One record—Jan. 26, 1935.

Ceophloeus pileatus pileatus (Linnaeus)—Pileated Woodpecker. The Pileated is fairly common in the deep pine woods 100 miles east of Dallas. It has been seen by at least six of the writer's friends close to the city of Dallas. Latest record is Dec. 25, 1934.

Centurus carolinus (Linnaeus)—Red-bellied Woodpecker. A common resident.

Melanerpes erythrocephalus (Linnaeus)—Red-headed Woodpecker. Common migrant and summer resident; Mar. 15,-Oct. 20. A few over winter.

Sphyrapicus varius varius (Linnaeus)—Yellow-bellied Sapsucker. Common migrant and winter resident.

Dryobates villosus villosus (Linnaeus)—Hairy Woodpecker. Fairly uncommon permanent resident.

Dryobates pubescens pubescens (Linnaeus)—Southern Downy Woodpecker. Common resident.

Dryobates scalaris symplectus (Oberholser)—Texas Woodpecker. Observed locally only since January, 1933.

PASSERIFORMES

Tyrannidae—Tyrant Flycatchers

Tyrannus tyrannus (Linnaeus)—Eastern Kingbird. Many breed here from April 13 to Sept. 5.

Tyrannus verticalis (Say)—Arkansas Kingbird. First seen on May 6, 1935.

Muscivora forficata (Gmelin)—Scissor-tailed Flycatcher. Common summer resident; April 2-Oct. 21.

Myiarchus crinitus crinitus (Linnaeus)—Crested Flycatcher. Especially common migrant, during April and May.

Sayornis phoebe (Latham)—Phoebe. Common summer resident; Mar. 16-Nov. 27. The Phoebe has been found wintering in the deep woods of East Texas.

Empidonax flaviventris (Baird and Baird)—Yellow-bellied Flycatcher. Uncommon May migrant; a few summer.

Empidonax virescens (Vieillot)—Acadian Flycatcher. A single record—May 9, 1931.

Empidonax minimus (Baird and Baird)—Least Flycatcher. Here commonly from May 3-Nov. 27.

Myiochanes virens (Linnaeus)—Eastern Wood Pewee. Uncommon summer resident; May 26-Nov. 27.

Nuttalornis mesoleucus (Lichtenstein)—Olive-sided Flycatcher. Recorded only once—May 9, 1930.

Alaudidae—Larks

Otocoris alpestris praticola (Henshaw)—Prairie Horned Lark. A not unusual winter visitant.

Hirundinidae—Swallows

Iridoprocne bicolor (Vieillot)—Tree Swallow. Uncommon. Only March and November records.

Riparia riparia riparia (Linnaeus)—Bank Swallow. Summer resident; April 15-Sept. 1.

Stelgidopteryx ruficollis serripennis (Audubon)—Rough-winged Swallow. Recorded Mar. 7, 1930 and then have been very common in the spring of 1935.

Hirundo erythrogaster (Boddaert)—Barn Swallow. Resident from April to late October.

Petrochelidon albifrons albifrons (Rafinesque)—Cliff Swallow. Uncommon resident; April 1-Sept. 30.

Progne subis subis (Linnaeus)—Purple Martin. A very common swallow from early March to late September.

Corvidae—Crows and Jays

Cyanocitta cristata cristata (Linnaeus)—Blue Jay. A common permanent resident.

Corvus brachyrhynchos brachyrhynchos (Brehm)—Crow. Common permanent resident.

Paridae—Titmice

Penthestes carolinensis agilis (Sennett)—Plumbeous Chickadee. Common permanent resident.

Baeolophus bicolor (Linnaeus)—Tufted Titmouse. Common permanent resident.

Sittidae—Typical Nuthatches

Sitta carolinensis carolinensis (Latham)—White-breasted Nuthatch. Observed on April 1, 1935.

Certhiidae—Creepers

Certhia familiaris americana (Bonaparte)—Brown Creeper. Common winter resident; Nov. 27-Mar. 25.

Troglodytidae—Wrens

Troglodytes aëdon aëdon (Vieillot)—House Wren. Common April and October migrant.

Nannus hiemalis hiemalis (Vieillot)—Winter Wren. Two records—Dec. 28, 1932 and Dec. 23, 1934.

Thryomanes bewicki bewicki (Audubon)—Bewick's Wren. Recorded twice—May 9, 1931 and Oct. 1, 1934.

Thryothorus ludovicianus ludovicianus (Latham)—Carolina Wren. This wren, our commonest, is fast becoming more abundant. A permanent resident.

Telmatodytes palustris palustris (Wilson)—Long-billed Marsh Wren. Fairly common in the White Rock marshes in March of 1929, but have not been reported since that date.

Mimidae—Mockingbirds and Thrashers

Mimus polyglottos polyglottos (Linnaeus)—Mockingbird. Common permanent resident.

Dumetella carolinensis (Linnaeus)—Catbird. The most unassuming of the *Mimidae*. We never realize this beautiful gray bird is capable of such an enchanting variety of notes until we force our way to his secluded perch. He likes to be close to man, but he likes to stay concealed. April 15-October 20.

Toxostoma rufum (Linnaeus)—Brown Thrasher. Abundant winter resident; Oct. 21-April 21.

Turdidae—Thrushes

Turdus migratorius migratorius (Linnaeus)—Eastern Robin. Some few winter in the deepest of our woods, but usually we find these augmented by a steady flock migrating throughout January, February, and March. The spring migration is very irregular. Some few pairs nest.

Hylocichla mustelina (Gmelin)—Wood Thrush. For some unexplained reason there is only one record of this bird—Mar. 25, 1930.

Hylocichla guttata faxoni (Bangs and Penard)—Hermit Thrush. Occasionally a few winter. Very early migrant; Jan. 26-May 5; and Oct. 1-Nov. 10.

Hylocichla ustulata swainsoni (Tschudi)—Olive-backed Thrush. Two records—April 24, 1929 and May 5, 1935.

Hylocichla fuscescens fuscescens (Stephens)—Veery. Fairly common migrant during May.

Sialia sialis sialis (Linnaeus)—Bluebird. A permanent resident.

Sylviidae—Gnatcatchers and Kinglets

Polioptila caerulea caerulea (Linnaeus)—Blue-gray Gnatcatcher. Found migrating during March, September, and November.

Regulus satrapa satrapa (Lichtenstein)—Golden-crowned Kinglet. Common winter resident.

Corthylio calendula calendula (Linnaeus)—Ruby-crowned Kinglet. Winter resident.

Motacillidae—Pipits

Anthus spinoletta rubescens (Tunstall)—American Pipit. An irregular winter visitor; however, they are usually to be found on the shore flats at White Rock at some time during every winter.

Bombycillidae—Waxwings

Bombycilla cedrorum (Vieillot)—Cedar Waxwing. Very common winter visitant, sometimes staying as late as May.

Laniidae—Shrikes

Lanius ludovicianus ludovicianus (Linnaeus)—Loggerhead Shrike. Common from September to April.

Sturnidae—Starlings

Sturnus vulgaris vulgaris (Linnaeus)—Starling. During the last few winters this bird has rapidly increased in numbers around Dallas. They were first observed in the winter of 1930. Dallas seems to be in the center of a winter area for great flocks that completely disappear in the summer.

Vireonidae—Vireos

Vireo atricapillus (Woodhouse)—Black-capped Vireo. An uncommon, but readily distinguishable species, found nesting here; April 1-Sept. 5.

Vireo griseus griseus (Boddaert)—White-eyed Vireo. Fairly common summer resident.

Vireo belli belli (Audubon)—Bell's Vireo. Fairly common summer resident; April 7-Aug. 21.

Vireo flavifrons (Vieillot)—Yellow-throated Vireo. Fairly common summer resident; April 1-Oct. 8.

Vireo solitarius solitarius (Wilson)—Blue-headed Vireo. Not uncommon migrant and winter resident.

Vireo flavoviridis flavoviridis (Cassin)—Yellow-green Vireo. Our commonest vireo; a summer resident from April 10-Oct. 20.

Vireo philadelphicus (Cassin)—Philadelphia Vireo. A rare summer resident and almost as rare a migrant; May 1-Sept. 11.

Vireo gilvus gilvus (Vieillot)—Warbling Vireo. Uncommon migrant; rarely breeds here.

Compsothlypidae—Wood Warblers

Mniotilta varia (Linnaeus)—Black-and-White Warbler. An uncommon migrant.

Protonotaria citrea (Boddaert)—Prothonotary Warbler. Seen both on the northern and eastern boundaries of Dallas County on Aug. 26, 1934.

Vermivora peregrina (Wilson)—Tennessee Warbler. Two records—April 25, 1929 and May 15, 1933.

Vermivora celata celata (Say)—Orange-crowned Warbler. Four were reported on Sept. 5, 1934.

Vermivora ruficapilla ruficapilla (Wilson)—Nashville Warbler. Never have been found nesting or as fall migrants. Spring records during April and May.

Compsothlypis americana pusilla (Wilson)—Northern Parula Warbler. One record—Mar. 31, 1935.

Dendroica aestiva aestiva (Gmelin)—Yellow Warbler. Common migrant and summer resident from April to October.

Dendroica magnolia (Wilson)—Magnolia Warbler. Common spring migrant. One unexplainable record on Dec. 26, 1932.

Dendroica tigrina (Gmelin)—Cape May Warbler. An unusual bird for this region. Two pairs were observed on April 28, 1935.

Dendroica caerulescens caerulescens (Gmelin)—Black-throated Blue Warbler. One of many warblers reported on May 15, 1933. This date signifies the height of the warbler migration for 1933.

Dendroica coronata (Linnaeus)—Myrtle Warbler. Fairly common winter resident and abundant migrant.

Dendroica virens virens (Gmelin)—Black-throated Green Warbler. Fairly common migrant.

Dendroica cerulea (Wilson)—Cerulean Warbler. Only one observation. This was of a nesting pair on April 17, 1932. The nest was of lichens and about twenty feet from the ground. There were four eggs.

Dendroica fusca (Müller)—Blackburnian Warblers. Numerous May records.

Dendroica dominica albilora (Ridgway)—Sycamore Warbler. One record—Mar. 31, 1935.

Dendroica pensylvanica (Linnaeus)—Chestnut-sided Warbler. A rather rare migrant.

Dendroica striata (Forster)—Black-poll Warbler. Common May 5-30. Only one fall record—Sept. 12.

Dendroica pinus pinus (Wilson)—Pine Warbler. Has for some reason always been an exceptionally early migrant. Mar. 19-April 21.

Seiurus motacilla (Vieillot)—Louisiana Water-thrush. Uncommon migrants; records from May 5-30.

Oporornis formosus (Wilson)—Kentucky Warbler. April 30, 1933.

Oporornis philadelphia (Wilson)—Mourning Warbler. Fairly common migrant; May 10-15.

Geothlypis trichas trichas (Linnaeus)—Maryland Yellow-throat. Common from May 1-Oct. 20.

Icteria virens virens (Linnaeus)—Yellow-breasted Chat. After hearing the Chat one would think he was some kind of a Mockingbird rather than a Warbler. Common as a May migrant; some few nest.

Wilsonia pusilla pusilla (Wilson)—Wilson's Warbler. May 17, 1933 and May 5, 1935.

Wilsonia canadensis (Linnaeus)—Canadian Warbler. One June record in 1929.

Setophaga ruticilla (Linnaeus)—Redstart. Common migrant; May 7-29.

Icteridae—Meadowlarks and Blackbirds

Dolichonyx oryzivorus (Linnaeus)—Bobolink. An uncommon migrant; one record—June 8, 1928.

Sturnella magna magna (Linnaeus)—Eastern Meadowlark. Common permanent resident.

Sturnella neglecta (Audubon)—Western Meadowlark. Not nearly as common as the preceding species.

Agelaius phoeniceus phoeniceus (Linnaeus)—Red-wing Blackbird. Common most all the year.

Icterus spurius (Linnaeus)—Orchard Oriole. Breeds here commonly, usually arriving about the middle of April.

Icterus galbula (Linnaeus)—Baltimore Oriole. Fairly common as migrant; April 28-May 15. Found one pair nesting at White Rock in 1934.

Euphagus carolinus (Müller)—Rusty Blackbird. The rarest of all Dallas Blackbirds.

Quiscalus quiscula aeneus (Ridgway)—Bronzed Grackle. Fairly uncommon permanent resident.

Molothrus ater ater (Boddaert)—Cowbird. Fairly common in summer and abundant in winter.

Thraupidae—Tanagers

Piranga erythromelas (Vieillot)—Scarlet Tanager. A beautiful rare migrant; one record May 21, 1931.

Piranga rubra rubra (Linnaeus)—Summer Tanager. Earliest record for this fairly common summer resident is April 21.

Fringillidae—Grosbeaks, Sparrows, and Finches

Richmondena cardinalis cardinalis (Linnaeus)—Cardinal. Common permanent resident.

Hedymeles ludovicianus (Linnaeus)—Rose-breasted Grosbeak. A very rare summer resident and migrant; one record—Apr. 25, 1929.

Guiraca caerulea caerulea (Linnaeus)—Blue Grosbeak. Fairly uncommon summer resident. April and May records.

Passerina cyanea (Linnaeus)—Indigo Bunting. Fairly common migrant; some few nest; April 1-Nov. 26.

Passerina ciris (Linnaeus)—Painted Bunting. Fairly common, arriving in April and leaving in September.

Spiza americana (Gmelin)—Dickcissel. Early migrant and common summer resident; April 17, Oct. 10.

Carpodacus purpureus purpureus (Gmelin)—Purple Finch. An irregular winter visitant; especially during December, January, and February.

Spinus tristis tristis (Linnaeus)—Goldfinch. Common winter resident.

Pipilo erythrophthalmus erythrophthalmus (Linnaeus) Towhee. A fairly common winter resident; Oct. 1-May 5.

Passerculus sandwichensis savanna (Wilson)—Savannah Sparrow. Fairly uncommon winter resident and migrant. It is possible that this bird is sometimes confused with *P. s. alaudinus* (The Western Savannah Sparrow).

Ammodramus savannarum australis (Maynard)—Grasshopper Sparrow. Common winter resident and migrant.

Passerherbulus caudacutus (Latham)—Leconte's Sparrow. Uncommon winter resident; Dec. 2-Mar. 23.

Passerherbulus henslowi henslowi (Audubon)—Henslow's Sparrow. Recorded every fall and winter since 1929.

Pooecetes gramineus gramineus (Gmelin)—Vesper Sparrow. Common as migrants; some few winter.

Chondestes grammacus grammacus (Say)—Lark Sparrow. Common in summer and not so common in winter.

Aimophila aestivalis bachmani (Audubon)—Bachman's Sparrow. A flock were seen here May 11, 1930 and another Feb. 6, 1932.

Junco hyemalis hyemalis (Linnaeus)—Junco. Abundant winter resident; Oct. 15-April 28.

Spizella arborea arborea (Wilson)—Tree Sparrow. Two records—Jan. 30, 1932 and Jan. 22, 1935.

Spizella passerina passerina (Bechstein)—Chipping Sparrow. One of our rare winter residents and fairly uncommon migrants.

Spizella pallida (Swainson)—Clay-colored Sparrow. Three records: Mar. 19, 1930, Feb. 5, 1932, and Oct. 28, 1934.

Spizella pusilla pusilla (Wilson)—Field Sparrow. Very common in winter some few summer.

Zonotrichia querula (Nuttall)—Harris Sparrow. Common winter resident; Nov. 19-April 3.

Zonotrichia leucophrys leucophrys (Forster)—White-crowned Sparrow. Uncommon in winter, abundant migrant, and rarely nesting.

Zonotrichia albicollis (Gmelin)—White-throated Sparrow. Much commoner than the preceding species at all times.

Passerella iliaca iliaca (Merrem)—Fox Sparrow. Fairly common. Sept. 20-April 13.

Melospiza lincolni lincolni (Audubon)—Lincoln Sparrow. One record—Mar. 10, 1930.

Melospiza georgiana (Latham)—Swamp Sparrow. Only two records—April 27, 1929 and Mar. 23, 1930.

Melospiza melodia melodia (Wilson)—Song Sparrow. Fairly common, especially among the reeds at White Rock.

SOUTHERN METHODIST UNIVERSITY,
DALLAS, TEXAS.

A STUDY OF THE RELATION OF THE DOUGLAS GROUND SQUIRREL TO THE VEGETATION AND OTHER ECOLOGICAL FACTORS IN WESTERN OREGON

ELTON R. EDGE

Introduction

Ecology in its broadest sense is generally defined as the study of the relationship between organisms and their environment. Shelford modifies this by defining ecology as the science of communities. Communal relations are of

Fig. 1. Douglas Ground Squirrel

undoubted importance and are obvious in vegetation and among many sessile animal forms but these relations are not so evident in the case of higher vertebrates. In this study the attempt was made to determine the relation of the Douglas ground squirrel, *Otospermophilus douglasii* (Rich.), (Fig. 1), to the various factors of the environment, particularly the vegetation.

Dominating all is the physical environment which will be considered only

in its broadest aspects. It is a complex of such factors as temperature, moisture, light, exposure, soil, and topographical features. The range of these factors are of the utmost importance for they determine the type of vegetation. Plants not only indicate the nature of the habitat but also the animals found in that habitat. The former directly by their presence and responses, and the latter, indirectly, by virtue of the control of plants over the food and shelter needs of the animal.

The biological factors of the environment which exists for the ground squirrel may be grouped under three rather broad headings: (1) the relation between the ground squirrel and the vegetation; (2) the inter-relation between the ground squirrels themselves; and (3) the relation between the ground squirrel and animals of different species.

In considering the relation between the ground squirrel and the vegetation, some repetition of already published material is considered necessary to convey a clear idea of the use of terms and of existing conditions. As already indicated the vegetation is considered of prime importance since it is both a habitat and an animal indicator. Certain plant forms are said to be dominant because they are the most important members of the community. They are able to modify and alter the physical conditions of the habitat and bring about changes which permit the invasion and monopolization of the changed habitat by the other plant forms. These new plant forms in turn modify the habitat and are likewise replaced by different forms. The ground squirrels are not adapted to all types of habitats, or major plant communities. They fit best into certain environments so that the succession which the vegetation brings about has an important bearing on their ability to maintain themselves. It is desirable, therefore, that the various developmental stages, associes, or seres through which the vegetation passes be considered.

In western Oregon much of the region can no longer be looked upon as primary area, or prisere, it has been more or less disturbed by man and must be considered secondary or subsere. The order of succession in this subsere is as follows: a coniferous area is swept by fire, the plant and animal life is destroyed, the soil is bared and no longer retains water, and a xerophytic habitat results. Weeds and certain grasses with efficient seed dispersal mechanisms settle in the area and a few of the more drought resistant forms gain a foothold. If the area is a rather dry one naturally, such as, the south side of a well drained hill, succession is much slower. After grasses and weeds have persisted for a time a few oaks and rose bushes are able to establish themselves here and there, spread rather slowly, and gradually modify conditions so that eventually Douglas fir seedlings find spots conditioned by the existing vegetation where they are able to survive. As the firs develop, more and more of them are able to enter the habitat, survive, shade the ground, and kill off and crowd out the grasses, other seed plants, the rose bushes and eventually the oaks, so that where once xerophitic conditions prevailed a mesophytic or rather moist habitat begins to form. Due to the shade tolerance of their seedlings, cedar and hemlock begin to invade the Douglas fir. The

cedar-hemlock invasion marks the appearance of the climax association, or because of its wide range and extent it might better be called the climax formation. The climax formation is a permanent condition as long as the existing climate lasts or until fire or the disturbing hand of man destroys it when the same cycle of development will be repeated.

Areas Studied

Three type areas (grass-weed or grassland, oak-rose, and invading Douglas fir) representing the three successional communities in which the squirrels were found, were chosen and their floral and faunal composition studied. The grass-weed or grassland area covered a section of level valley land over an acre in extent about three miles northeast of Eugene, Oregon, (Fig. 2). This

Fig. 2. Grass-weed Community

area had not been cultivated or disturbed for a number of years. A number of oak-rose areas were investigated but the one which received most attention was on the rolling hills about six miles southwest of Eugene, (Fig. 3). The invading Douglas fir area chosen was located on Coburg hills about four miles north of Eugene, (Fig. 4). This area was a subsere development, indicated by the blackened remains of old stumps left by wood cutting and lumbering operations followed by fire which swept bare five or six acres of the hillside. This appeared to have taken place about ten years prior to the time of this study for the bare area had grass, weeds, numerous shrubs, and bushes; but not many oaks because rather moist conditions, and already modified soil had permitted relatively rapid development. Many young firs were invading the area.

Methods

It is believed that the taxonomic composition of these areas as determined is reasonably accurate and adequate for the purpose of bringing out the position of the ground squirrel in the biome. Instead of counting a number of quadrants on a transect through the area, the area was cruised and a number of apparently typical quadrants counted by the frequency method. A relatively large area seemed more suitable for mammal census so the woody perennials were converted to the same unit area, forty ares.

Fig. 3. Oak-rose Community showing slow invasion by Douglas Fir

An are is equal to a ten meter square or .025 acre. On account of their large numbers, the herbaceous annuals and perennials were based on a much smaller unit area, one four-hundredth are. The seasonal aspect of the herbaceous forms was not investigated as the quadrant studies were made in the late summer, however, it is believed no important vernal forms were overlooked as dry seed stalks of forms considerably past maturity were counted. Prof. L. F. Henderson, Curator of the University of Oregon herbarium, identified the forms which were doubtful.

To arrive at any numerical concept of the fauna was a much more difficult undertaking. Taylor (1930) mentions a number of methods for determining animal population but even a combination of them does not give the accuracy obtainable in plant work. The method used in this investigation consisted of a combination of trapping, observation, and den counts. The figures given for the Douglas ground squirrel are for late spring before any of the young had appeared. The number seems to be fairly constant each

year for a given area under normal conditions. In trapping the squirrels, steel traps were placed in the burrow entrance. For the smaller rodents, Biological-Survey model snap traps were used. Artificial bait, Anthony (1925), was generally used on the small traps. Weed seeds similar to those found in the cheek pouches of the squirrels were also found very effective. The effectiveness of these shows a definite competition for feed between the squirrels and other forms.

Insects were collected a few times from unit areas but due to lack of taxonomic facilities this work was not continued. Insects do not seem to be

Fig. 4. Invading Douglas Fir Area (Rapid Succession)

of very great importance with respect to ground squirrels. However, such forms as grasshoppers, ants, and under favorable conditions moths and butterflies with their resulting caterpillars, might exert an appreciable effect in the environment.

On account of the frequent movements of birds it was not possible to assign a numerical value to them. The qualifying terms given are based on numerous one-half to one hour visits to the different areas. Transients which did not seem to be feeding in the areas were omitted. The term "C" indicates those forms which were observed quite frequntly, "O" indicates occasionally observed, possibly once in five visits, "R" indicates rare.

TABLE 1

Numerical List of Vegetation in Different Communities.

Herbaceous plants, Unit area 1/400 are	Grassweed	Oakrose	Invading fir
Plantago lanceolata L. Plaintain	22		5
Hypochoeris radicata L. False Dandelion	18		5
Aspris sp.? and *Agrostis* sp.? Tickle Grass	13	50	

Notholcus lanatus Nash. Velvet Grass	5		7
Bromus sp.? Brome	5	22	
Bromus secalinus L. Cheat	3		
Erodium cicutarium L'Her. Filaree	3	2	
Pteris aquilina L. Bracken Fern	2		
Hypericum perforatum L. St. John's Wort	3		2
Equisetum arvense L. Horsetail	3		
Avena sativa? Oats	1		
Daucus carota L. Wild Carrot	1		
Malva rotundifolia L. Mallow	x		x
Rumex acetosella L. Sorrel	x		
Iris tenax Dougl. Blue Flag	x		1
Hordeum pusillum Nutt. Dwarf Barley		10	
Navarretia squarrosa H. & A. Skunk Weed		15	
Madia glomerata Hook. Tarweed		3	
Epilobium paniculatum Nutt. Fireweed		3	
Lupinus albicaulis Dougl. Blue Lupine			1
Cirsium lanceolatum (L.) Bull Thistle			x
x=less than one, that is, average is less than one.			
Woody perennials, Unit area 40 ares (1 acre)			
Quercus garryana Dougl. White Oak		40	15
Rosa rubiginosa L. some *R. nutkana* Pres. Rose		40	
Rhus diversiloba T. & G. Poison Oak		30	150
Corylus rostrata Ait. Hazel			150
Pseudotsuga taxifolia (Poir.) Douglas Fir			70
Ribes sanguineum Pursh. Wild Currant			60
Sambucus glauca Nutt. Elder			50
Rubus leucodermis Dougl. Black Cap			40
Berberis aquifolium Pursh. Oregon Grape			40
Acer macrophyllum Pursh. Maple			30
Osmaronia cerasiformis (T. & G.) Osoberry			30
Arbutus menziesii Pursh. Madrone			20
Symphoricarpos racemosus Mich. Snowberry			20
Amelanchier alnifolia Nutt. Service Berry			10

TABLE 2

Numerical List of Fauna in Different Communities.

Mammals, unit area 40 ares (1 acre)	Grassweed	Oakrose	Invading fir
Otospermophilus douglasii (Rich.) Douglas Ground Squirrel	15	15	18
Microtus townsendii (Bach.) Meadow Mouse	5		
Mus m. musculus L. House Mouse	3		
Mephitis o. spissigrada (Bangs) Str. Skunk	.01	.02	.05
Peromyscus m. rubidus (Osg.) White-footed Mouse	20	20	24
Thomomys bulbivorus (Rich.) Pocket Gopher	3	3	5
Canis l. lestes Mer. Coyote		.001	?
Lepus c. californicus Gray, Jack Rabbit		.05	
Sylvilagus b. ubericolor (Mil.) Brush Rabbit			.4
Mustela sp.? Weasel		.01	?
Urocyon c. townsendi? (Mer.) Gray Fox			?
Lynx r. fasciatus Raf. N.W. Wildcat			?
Birds feeding in the area			
Passer d. domesticus L. English Sparrow	C	--	--
Euphagus cyanocephalus (Wagl.) Brew. Blackbird	O	O	
Spinus t. salicamans Grin. Willow Goldfinch	O	O	O
Otocoris a. strigata Hen. Horned Lark	R	R	

Phasianus c. torguatus Gmel. Pheasant	O	R	
Buteo b. calurus Cas. Red-tailed Hawk	R	O	C
Falco s. phalaena (Les.) D. Sparrow Hawk	C	O	C
Passerculus s. aludinus Bon. Savannah Sparrow	O	O	
Pooecetes g. affinis (Mil.) O. Vesper Sparrow	O	O	O
Lophortyx c. californica (Shaw) Calif. Quail	R	R	O
Sturnella neglecta (Aud.) W. Meadowlark	O	O	R
Zenaidura m. marginella (Wood.) Mourning Dove	O	O	O
Colaptes c. cafer (Gmel.) N. W. Flicker		O	O
Spizella p. arizonae Coues W. Chip. Sparrow			O
Sialia m. occidentalis Town. W. Bluebird			O
Corvus b. hesperis Ridg. W. Crow		O	O
Turdus m. propinquus Ridg. W. Robin			O
Owl pellets, probably *Bubo v. saturatus* Ridg.			O
Snakes seen near burrows			
Crotalus oreganus Holb. Rattlesnake		R	
Pituophis c. catenifer (Blain.) Gopher Snake		O	R

Relation of Ground Squirrels to Plant Communities

When the squirrels are considered with reference to the vegetation, it is found that they favor the relatively dry habitats or xeroseres; such as the grass-weed, the oak-rose, and the invading Douglas fir. The mesophytic habitats; Douglas fir, and cedar-hemlock, are invaded by the squirrels only when they border on one of the three previously mentioned habitats. In any of the habitats occupied by the ground squirrel the slope or nature of the ground must permit drainage so that an accumulation of ground water does not drown out the squirrel during the rainy season.

The number of ground squirrels per unit area in the different communities studied is larger than could be expected for great areas of similar territory. Grinnell estimates one per acre for the closely related Beechey ground squirrel in California. The grassland or gravel-pit association studied, probably supported a larger number of squirrels than would normally be expected due to the proximity of oat and grain fields. The oak-rose area studied represents about normal conditions for the squirrels even though stock was pastured there. The invading-fir area on Coburg hills, in spite of the beginning of unfavorable conditions, supports a larger population per unit area than either of the others and greater than could normally be expected of this habitat on account of its fertile soil and consequent greater food productivity.

The question arises, why are the squirrels found in the xerophytic and not in the mesophytic habitats? The ground squirrels are in the xerophytic habitats because in them they find the grasses, seed plants, and shrubs on which they live at their best, and optimum conditions for the squirrels are present. They may live for a time in timber but they must be able to reach some open area where their type of food is available.

A check of food materials found in the squirrel's cheek pouches, burrows, and stomach when it could be identified, showed a very close relation to the plant environment. In the spring, this food material consisted of succulent grasses, leaves of velvet grass, certain cheats, clover, filaree, and false dandelion; and later in the year the heads and seeds of the false dandelion,

plantain, lupine, rose, filaree, tarweed, St. John's wort, fireweed, oats, wheat, barley and the like as well as acorns, hazelnuts, walnuts, cherry and prune pits. The cyclic change of food from grasses in the spring to a more concentrated type of food in the late summer and fall no doubt largely accounts for the heavy layer of fat these rodents put on late in the season just prior to their inactive period.

Relation of Ground Squirrels to Each Other

In spite of the fact that individuals of the same species are in direct competition with each other for food, space, and mates they tend to congregate together. The site of a large number of burrows soon gets cleared of food so that the squirrels must make quite extensive trips afield. Well beaten runways are found which are a hundred or more feet in length. Long trips for food expose the squirrels to enemies in the air and on the ground. The gregarious tendency, however, does have some advantage for the warning note of one squirrel sets the others on the alert or scurrying for their burrows. An acre may have about fifteen ground squirrels on it in the spring and due to the presence of young about fifty in the late summer. This congestion of population may in part account for the tendency of the squirrels to wander long distances in the fall. They spread into and try out all sorts of habitats, many of which do not prove suitable and as a result these squirrels do not survive. Close association of the same species facilitates the spread of parasites and disease. The parasites found on the skin and in the ears and nasal cavities, consisted of fleas, *Ceratophyllus acutus* Baker, louse *Polypeax spinulosus* Burmeister, tick *Margaropus annulatus* Say, mite *Lealops* sp.? The fleas are the predominating forms though the mites may exceed them in actual numbers. A scrawny mangy animal is generally heavily infested with fleas. Probably all the parasites vary in number with the locality, season, and physical condition of the animal. The mites causing mange and skin diseases were not investigated. Examination of the digestive tract, lungs, and other related structures were made a number of times, and several forms were found but their taxonomic position was carried no farther than to the large general group to which they belonged, i.e., several nematodes, at least two flagellated protozoans, and probably a cestode. No parasites were found in the blood, coelom, muscular or connective tissue.

Relation of Ground Squirrels to Other Species

The third relationship is that of the ground squirrel to other species. These species may be classed under two headings: (1) those which are competitors for food and territory, and (2) those which are predatory enemies. As already stated the giving of a numerical value to different species had to be based on a number of criteria. The values given are probably nearer correct for the herbivora than for the carnivora. The latter are naturally much fewer in numbers, and are wider ranging animals. It was found that six or eight whitefooted mice could usually be taken where only three or four ground squirrels were taken, but this number of mice might be discounted a little

on account of baited traps being used for mice and unbaited steel traps for the squirrels. The white footed mice appear to offer considerable competition for food. The gopher offers the squirrel a little competition for territory, and food; but since its numbers are relatively fewer in the same territory, the competition is not serious. The other rodents mentioned in Table 2 are not considered serious competitors unless a series of favorable circumstances occur which permit the development of excessive numbers which might occur in the case of meadow mice or jackrabbits. A number of seed-eating birds like the mourning dove and some of the sparrows offer considerable competition for food, but this does not appear to be serious under average conditions. The squirrel gets ahead of some of these transient visitors by being continually on location and getting the seeds even before some are mature. In this region the larger congregations of burrows are in pasture land, so that cattle and sheep probably take a large share of the available food making competition all the keener among the endemic population. The stock serves to hold the pastured area in a near xerophytic condition and checks the advance of new plants, bushes, or trees which if they gained a foothold would tend to change the habitat into a mesophytic type with reduction in seed plants and grasses, and make it a more unfavorable habitat for the squirrels.

We come now to a consideration of the predatory enemies, preying upon the squirrels for food. When the number of squirrels taken by predators is not excessive the effect may be more beneficial than harmful to squirrels, because the sick or less alert are the most likely to be taken. Among the birds, the large hawks probably take the heaviest toll of squirrels. The red-tailed hawk was the one most frequently observed in the areas studied but its capture of a ground squirrel was noted only once. The crow was occasionally seen in the neighborhood of burrows and no doubt picks up some of the young. In eastern Oregon several of the trapped squirrels were killed and partly eaten by ravens. Snakes probably take a few squirrels. Rattlesnakes were reported in the neighborhood of the oak-rose area by ranchers living near there. Two gopher snakes, *Pituophis* were captured in squirrel areas. This large snake is quite capable of mastering a young ground squirrel but probably devotes most of its attention to smaller rodents.

Among the predatory mammals in western Oregon, cats and roving dogs can be credited with killing many squirrels. Skunks are fairly numerous, three were taken in traps set for squirrels. Since a large part of their hunting is done at night they probably get only a few of the young squirrels and those in shallow burrows. The coyote is no doubt able to secure quite a number of squirrels, but they are no longer numerous in this part of Oregon. Weasels are reported in this region and what appeared to be one was seen in the oak-rose area, the extent of their depredations on squirrels is not known. In digging out burrows, parts of squirrel skeletons were often found, whether some animal kills them in the burrows or they died of disease could not be determined. Wild cats and foxes are reported from the Coburg hills region but they are probably not numerous enough to make any serious inroads on the squirrel population.

Man should head the list as the squirrel's chief enemy in spite of the fact that it is he who brought about the environmental changes which are favorable for their multiplication. Where careful poisoning and repoisoning are done early in the spring more than ninety percent of the squirrels are killed.

Fig V
FOOD RELATIONS AND INFLUENCING FACTORS
Size of block indicates only in a very general way the magnitude of the influence

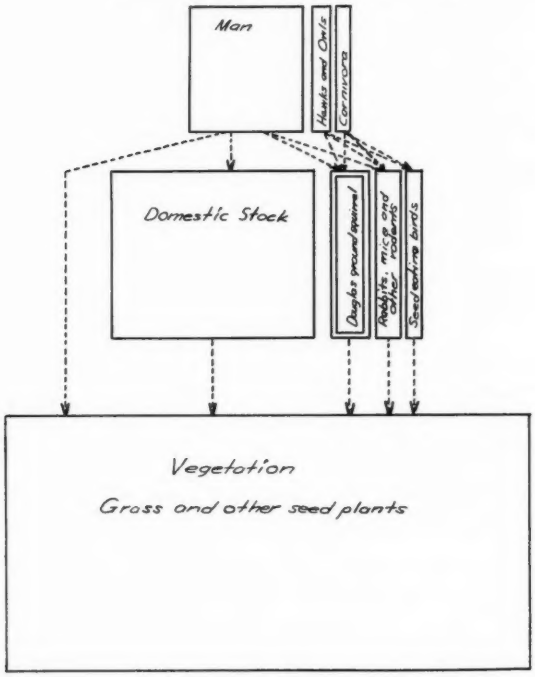


Fig. 5 shows roughly the pyramiding of numbers, and the general relationships which exist between the various members of the community.

Summary

1. The suitability of an area for Douglas squirrel occupation is indicated by the vegetation.

2. In Western Oregon the ground squirrels are found in the xeroseres and drop out when Douglas fir has taken over the habitat.

3. The xeroseres support a good crop of grasses and other seed plants which are food for the ground squirrels.

4. Competition for food is offered by mice, other rodents, rabbits, and seed-eating birds. Domestic stock hold back developmental succession in the habitat, but may cut down the food supply so that food competition for the squirrel becomes critical.

5. Predatory enemies, take a heavy toll of the ground squirrels.

6. Man is the most important single factor in the squirrel situation for he modifies the habitat, usually towards greater suitability for the squirrel, but he also, by poisoning, cleans out whole populations of squirrels in restricted areas.

REFERENCES

ANTHONY, H. E. 1925—Capture and preservation of small mammals. Am. Mus. Guide, Leaflet 61, 2nd ed., p. 1-35.

EDGE, ELTON R. 1934—Burrows and burrowing habits of the Douglas Ground Squirrel. J. Mammalogy **15**(3):189-193.

GRINNELL, J. AND J. DIXON. 1918—California Ground Squirrels. State Com. Horticulture Bull. **7**:596-807.

HOFMAN, J. V. 1920—The establishment of a Douglas Fir forest. Ecology **1**:49-53.

SHELFORD, V. E. 1932—Basic principles of classification of habitats and uses of terms. Ecology **13**:105-120.

TAYLOR, W. P. 1930—Methods of determining Rodent pressure on range. Ecology **11**:523-542.

SAN BERNARDINO VALLEY JUNIOR COLLEGE,
SAN BERNARDINO, CALIFORNIA.

THE ABNORMAL GROWTH OF THE MOLAR TEETH AND THE FRONT CLAWS OF AN ADULT POCKET GOPHER, GEOMYS BURSARIUS (SHAW)*

OTIS WADE AND PAUL T. GILBERT

A male pocket gopher recently added to the collection of the Zoology Department of the University of Nebraska showed unusual abnormalties of the molars and excessive growth of the front claws for an animal otherwise apparently normal. The accompanying illustrations show this condition more clearly.

Fig. 1

Fig. 2

Fig. 3

This specimen was taken by Mr. W. E. Beed near Lincoln, Nebraska, March 15, 1934. It had the following measurements: length 300 millimeters, tail 94 millimeters, hind foot 38 millimeters, which show that it was fully mature and of average size for males of this species. It was in good flesh and apparently active and doing well in spite of the condition of the structures mentioned.

The incisors were normal and showed that they had been regularly used. The molars above and below, had so grown out of line, however, that certain ones were crowded to one side where they could not be used effectively. The greatest divergence occurred in the upper series; here the second molars are so far out of line that they were only partly functional and probably were troublesome. They project outward sharply and have grown quite long and snag-like. Their medial surfaces were worn down some, forming a cutting face, which indicates some use and also that this prevented the excessive growth with what would have been disastrous results.

In chewing, use was made more of the pre-molars and the left first maxillary molar, aided some by the third upper molars. The right first maxillary molar was very short and not used; it was suppressed and overgrown by the premolar. In the picture it does not show as it is deep and obscured by the others. Its mate tends to be crowded outward and was able to develop.

* Studies from the Zoological Laboratory of the University of Nebraska, No. 184.

Attention is directed to the manner in which the second upper molars have been crowded to one side by the encroaching teeth in front, principally the premolars; the left first upper molar is also involved in this displacement. The last molars have altered their position some by leaning forward somewhat to compensate for the second molars, missing out of line. Thus the chewing surface is fairly continuous and slopes distinctly downward from front to rear (note side view).

In the mandible the molars are interestingly adjusted to accommodate their contact surfaces to the ones above. In this series both the first and

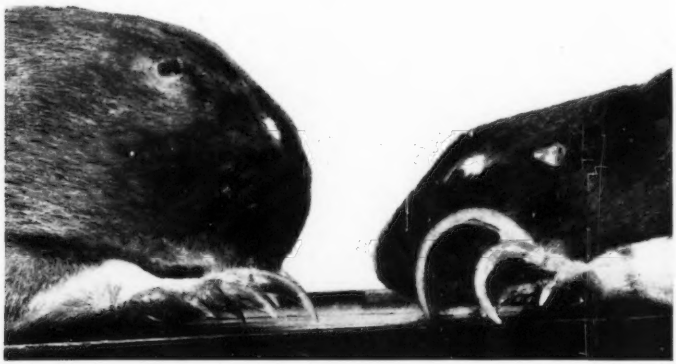


Fig. 4

second molars are quite out of line, but crowded inward acutely instead of outward as obtained in the maxillary series, and they were used, their crowns showing this plainly, thus preventing undue growth in length.

Here again the last molars lean forward even more, past the ones immediately in front, tending to bridge the gap caused by the incrowding of the first and second molars. The grinding surface of the last pair of molars is increased and slopes backward because of their altered position. The mandibular premolars, likewise have their crowns sloping distinctly downward toward the rear and a corresponding increase in chewing surface. The left one is especially prominent with a sharp-pointed, forward termination.

On the front feet the claws are unduly lengthened and slender. The second and third claws are very long, sharp and sickle-shaped. This would indicate that they were probably not much used for digging. The animal may have used its incisors a great deal for digging or else resorted to the use of abandoned runways or occupied those of others. In the photograph normal claws of another individual (left) are shown for comparison.

Department of Zoology and Anatomy,
University of Nebraska,
Lincoln, Nebraska.

HOMONYMS AND NOMENCLATORS

PAUL H. OEHSER

Systematic zoologists the world over will welcome the announcement by the Council of the Zoological Society of London of its plans for the preparation of as complete a list as possible of all generic names that have been used in Zoology from the tenth edition of Linnaeus through 1935. It is estimated that nearly 200,000 names will be included, and 1937 has been set as a possible publication year. The society has invited all systematists and others interested in the production of such a work to report any names of genera or subgenera (with reference to the original place of publication) that appear to have been omitted from existing records or catalogues.

This work, especially if it can be brought out at a price moderate enough to assure wide distribution among zoologists and libraries, will go a long way toward reducing the number of homonyms in zoological nomenclature. Homonyms, or names found to be preoccupied elsewhere in Zoology, are one of the impedimenta that clutter up taxonomy; and there are altogether too many of them. (I have found more than a dozen myself in the past year, and I see only a small part of taxonomic literature.) In the case of species and subspecies, homonyms occur relatively infrequently, but not so with genera, for generic names seem to be very scarce, judged by the many instances of preoccupation that occur and subsequently have to be corrected under Article 34 of the International Rules of Zoological Nomenclature.* It must not only be rather embarrassing for an author to discover or be told that his proposed name is preoccupied, but for all concerned it is a nuisance and an expense to make the corrections required. In cases where the homonym is not discovered until after the name has been published sometimes in many places, the awkwardness of it is all the more evident.

Homonyms are usually inadvertent and result from the lack of any systematic attempt on the part of the author to make certain that his proposed name is available. Perhaps he does not have the necessary reference books readily at hand, or, having consulted one nomenclator, he takes that as final. In other cases he may not know just where to look. It may serve a very useful purpose, therefore, to list together here the most important zoological nomenclators, so that an author may be reasonably certain that he has exhausted the possibilities in checking individual names, particularly genera. The chief works of this kind are as follows:

Agassiz. Louis.
1842-46. Nomenclator zoologicus, continens nomina systematica generum animalium tam viventium quam fossilium, etc., 26 fasc. by class, paged separately. Solothurn.
1846. Nomenclatoris zoologici index universalis, 393 pp. 4°. Issued with preceding.
1848. Idem. Issued in 12°.

* The International Rules of Zoological Nomenclature, with a summary of Opinions 1-90 rendered by the International Commission, have been published in Proc. Biol. Soc. Washington **39**:75-103, July 30, 1926. The Opinions in full are published by the Smithsonian Institution.

Carus, J. Victor, and Korschelt, Eugen (editors).

1889-1929. Register zum Zoologischen Anzeiger. 8 vols. (for vols. 1-75 of the Zool. Anz.), published as follows: 1889, 1893, 1899, 1903, 1908, 1913, 1922, and 1929. Leipzig.

Marschall, August Friedrich.

1873. Nomenclator zoologicus, continens nomina systematica animalium tam viventium quam fossilium, etc., 482 pp. Vindobona.

Scudder, Samuel Hubbard.

1882. Nomenclator zoologicus: An alphabetical list of all generic names that have been employed by naturalists for recent and fossil animals from the earliest times to the close of the year 1879. U. S. Nat. Mus. Bull. **19**, in 2 pts.: I, Supplemental list; II, Universal index; 376 + 340 pp. Washington.

Sherborn, Charles Davies.

1902. Index animalium sive index nominum quae ab A.D. MDCCLVIII generibus et speciebus animalium imposita sunt, sect. 1 (1758-1800), 1,195 pp. London.

1903-33. Idem, sect. 2 (1801-1850), in 33 pts., 1,198 pp.

Schulze, Franz Eilhard, and Kükenthal, Willy.

1926-date. Nomenclator animalium generum et subgenerum. Edited by Th. Kuhkgatz. Published by the Preussische Akademie der Wissenschaften, Berlin. (Now in its 4th vol.).

Waterhouse, Charles Owen.

1902. Index zoologicus, No. 1: An alphabetical list of names of genera and subgenera proposed for use in zoology as recorded in the "Zoological Record". . . (1880-1900) together with other names. . . ., 421 pp. London.

1912. Idem, No. 2 (1901-1910), 324 pp.
(Names recorded in the Zoological Record since 1910 may be found by consulting the indexes of that periodical beginning with vol. 48.)

In addition to the foregoing there are many lists of genera used within various restricted zoological groups, chief of which are as follows:

Bronn, Heinrich Georg.

1848-49. Index palaeontologicus oder Übersicht der bis jetzt bekannten fossilen Organismen, etc.: A Nomenclator palaeontologicus, in alphabetischer Ordnung. 2 vols.: 1,381 + 1,106 pp. Stuttgart.

Jordan, David Starr.

1917-20. The genera of fishes, 1758-1920, with the accepted type of each. Leland Stanford Jr. Univ. Publ., Univ. Ser., 4 pts., 576 pp. + indexes.

McGregor, Richard Crittenden.

1920. Index to the genera of birds. Philippine Dept. Agr. and Nat. Res. Publ. **14**, 185 pp. Bureau of Science, Manila.

Palmer, Theodore Sherman.

1904. Index generum mammalium. A list of the genera and families of mammals. North Amer. Fauna **23**, 984 pp. Washington.

Quenstedt, W. (editor).

1913-date. Fossilium catalogus. I, Animalium. 69 pts., each by different author, now issued; others in preparation. Berlin and 's-Gravenhage.

Richmond, Charles Wallace.

1902. List of generic terms proposed for birds during the years 1890 to 1900, inclusive, to which are added names omitted by Waterhouse in his "Index Generum Avium." Proc. U. S. Nat. Mus. **24**: 663-729. Washington.

1908-27. (The foregoing list was supplemented and brought to date as follows: Proc. U. S. Nat. Mus. **35**:583-655, 1908; **53**:565-636, 1917; **70**(art. 15):1-44, 1927.)

Sherborn, Charles Davies.

1893-96. An index to the genera and species of the Foraminifera. Smithsonian Misc. Coll. **37**:1-485. Washington.

Stiles, Charles Wardell, and Hassall, Albert.

1908-20. Index-catalogue of medical and veterinary zoology. Hyg. Lab. U. S. Public Health Service Bull. **37**, 401 pp., 1908 (Trematodes); Bull. **85**, 467 pp., 1912 (Cestoda and Cestodaria); Bull. **114**, 886 pp., 1920 (Roundworms). Washington.

Waterhouse, Frederick Herschel.

1889. Index generum avium. A list of the genera and subgenera of birds, 240 pp. London.

The Sherborn Index Animalium (so far as it goes—1850) and the Schulze and Kükenthal Nomenclator (so far as it has appeared—through the letter P) are the most recently published and are intended to supersede all previous nomenclators. Unfortunately, there are always omissions, and zoological nomenclature never ceases, so a nomenclator is never up to date. That is why no one can ever be absolutely sure of a name. We wonder, though, whether authors are not often less careful in checking their proposed names than they are in verifying their scientific data before publication. There is no argument, of course, as to which is relatively the more important, but certainly conscientious adherence to the rules of zoological nomenclature is a help rather than a hindrance to systematic knowledge of the natural world. And what might seem to be an inordinate amount of work required in tracing down a single name is nothing when compared with the endless explanations, corrections, and annoyances resulting when a name has to be rejected because it is preoccupied. The responsibility lies with the author, and it is for the purpose of helping him that the foregoing list of nomenclators is presented.

SMITHSONIAN INSTITUTION,
WASHINGTON, D. C.

Book Reviews

HANDBUCH DER PALAEORNITHOLOGIE, von Kalman Lambrecht. Berlin: Gebrüder Borntraeger, 1933. xix+1024 pp., 209 figs. in text, 4pls. RM 115.

This large volume, the result of many years' work in compilation and personal investigation by Professor Lambrecht, is an encyclopedic summary of man's knowledge of fossil birds, considered from the systematic, stratigraphic, distributional, phylogenetic and palaeobiological points of view. Preceded by Lambrecht's "History and Bibliography of Palaeornithology" (1916, Aquila, Vol. 23, pp. 196-307, 483-501) and his catalog of fossil birds (1921, Fossilium Catalogus. 1: Animalia; Pars 12: Aves) it represents the very first attempt to gather in one volume all the information on fossil birds which, through the years, has been accumulating in numerous, scattered publications.

Even a cursory glance at the contents reveals the wide scope and the comprehensive organization of the work. The first section, which constitutes an osteological introduction, reviews briefly the known fossil material and the comparative osteological collections of the world. There is a series of line drawings illustrating, from fossil material, the various skeletal elements, with a comprehensive bibliography arranged according to elements. The bibliography for the sternum, for example, includes forty-three titles. Modern Latin, English and French terms are given for the parts.

Roughly two-thirds of the book are devoted to the systematic section, under the title, "Das fossile Material." The classification follows, in principle, Wetmore's recent modification of Gadow's system, differing chiefly in the absence of any sub-class or superordinal designations and in the treatment of the Cretaceous toothed birds. Proceeding on the belief that the presence of teeth is not of extreme importance and that the morphological similarities these forms show to certain "neognath" orders are too numerous to be due to parallelism, the Hesperornithiformes are placed next to the Colymbo-Podicipediformes, the Ichthyornithiformes next the Telmatoformes. The fossil genera *Gastornis*, *Remiornis*, *Dasornis* and *Macrornis* are provisionally united with the genera *Diatryma* and *Omorhamphus* to form the order Diatrymiformes.

The fossil species are treated systematically, under thirty-two orders, with subheadings for families and genera. Diagnoses of major groups are given, and for each species there is a resumé of specific characters with frequent direct quotations, an enumeration of known material, and a statement as to geologic age and locality of occurrence. The treatment of each order is introduced by a bibliography pertaining to the osteology of that order. Extensive discussion is accorded such groups as Archaeornithiformes to include the history of individual specimens, purchase prices, etc. Some groups are critically revised, insofar as was possible through examination of material in Old World museums. Among the better examples of phylogenies indicated are those of the cormorants, flamingoes, penguins and storks. Particularly valuable are some of his opinions on material from the Tertiary of France.

The third section, devoted to stratigraphy, reviews the avian faunae of the various geologic periods, chronologically treated and, where feasible, geographically arranged. This section closes with an extensive bibliography of upper Pliocene, Pleistocene and sub-fossil forms with exceedingly useful faunal lists for these epochs.

The final section deals, under the heading "Allgemeine Palaeontologie und Palaeobiologie," with numerous general questions and some inevitable speculations. Several pages are devoted to such topics as fossilization of bird remains, causes of death, preservation of soft parts, feather impressions, footprints, eggs, etc. The meat of this section however, is contained in the discussion of adaptations and of avian phylogenies. Adaptations to flying, to swimming and diving, and to the terrestrial and arboreal modes of life are reviewed in some detail, as also the methods for securing food. There is very little palaeontology in this part, but it is a valuable guide to the work done in the field of adaptations and is supported by numerous references. There is, finally, a consideration of the proavis problem, a review of the theories as to the nature of the hypothetical ancestral bird, the author generally favoring a primary cursorial type,

with subsequent arboreal adaptations. No new theory is advanced, in the belief that further speculation must await more evidence. The work is brought to a close with a discussion of the problem of "Ratite" affinities, in which Lambrecht takes issue with the views of Lowe, insisting on origin from ancestors capable of flight and implying polyphyletic derivation of the group.

An invaluable feature of this work is the presentation of extensive and comprehensive bibliographies. Arranged chronologically and according to subject, with more important papers emphasized through the use of bold-face type, they form a reference source that can be appreciated properly only through use. The book is indexed in an unusually thorough manner; no less than seven separate indices, to topics, to localities, geological formations, museums and collections, authors, illustrations and to genera and species, simplify the task of finding any desired bit of information and enhance the value of an already valuable work by rendering it exceedingly useable. Profusely illustrated, well-printed on good paper, this is a work which no specialist can afford to be without, since it now may be taken as the starting point for all avian palaeontological studies. It is, moreover, a book which will prove its usefulness to anyone dealing with birds or with the higher vertebrates generally.—WILLIAM L. ENGELS and ALDEN H. MILLER, University of California, Berkeley.

THE ARACHNIDA, by Theodore H. Savory. Edward Arnold & Co. London. Published in the United States by Longmans, Green & Co. vii+218 pp., 8 pl., 99 figs. Price, $8.50.

The author states in the preface that his purpose in writing this book is to make "a first attempt to give Arachnology something of the unity and status of an individual science that is possessed by Entomology." The attempt seems to have been successful. The volume bears the marks of sound scholarship and, on the mechanical side, of superior craftsmanship. It is the only book of its kind known to the reviewer which preserves a balance of treatment among the various orders of the Arachnida, all the other works putting an overwhelming emphasis on the order to which the spiders belong. The treament is divided into three parts. The first part describes the Arachnida as a whole—their structure, habits, distribution, phylogeny and classification. The second part is a detailed account of the various orders, including fossil forms. The classification is carried down to the families. The third part includes economic, practical and historical considerations. There are three indices and a good table of contents.—F. WENNINGER.

LIMNOLOGY, by Paul S. Welch. New York, McGraw-Hill Book Co. 1935 xiv+471 pp. $5.00.

Limnology, as here understood, includes the study of all inland bodies of water, especially those containing fresh water. Because this is a new science there is as yet no thoroughly adequate text book—at least, in English. This volume undertakes to acquaint the student with the various relations that exist between plant and animal organisms and their aquatic environs. Much information has accumulated in various countries and is deposited in numerous scientific journals and special treatises. An attempt has been made to gather into this book all the essential facts of limnology and to present these for class use. Original work of the author and his associates is included and gives to the book a characteristic note. Because a special volume on method is in preparation by the author, this subject receives only cursory notice in this volume.

A departure from conventional treatment as found in ecological works of a more general nature is the use in this volume of much new material. This fact will be appreciated especially by those who have always regretted the superficial and inadequate treatment that this phase of ecological investigation has too often received.

Ecologists will therefore be grateful to Dr. Welch for this admirable guide for the investigation of a much neglected habitat group. This book should be a stimulant for further work towards a better understanding of limnological phenomena and, through them, of general biological problems.—TH. JUST.

A MONOGRAPHIC REARRANGEMENT OF LOPHODERMIUM, by L. R. Tehon. Illinois Biol. Monographs **13**(4):1-151. Pls. 1-5. August 1935.

The species of the genus Lophodermium because of their economic significance as inhabitants of the needles of evergreens and their uncertain taxonomic position among the fungi lend themselves to profitable study.

After a review of the history of the genus from its establishment in 1926 by Chevallier the author confines his treatment to the species remaining in the genus which is described as having elongated ascomata which open by means of elongated ostioles surrounded by thickened or carbonized labia and lined with periphyses. The asci are cylindrical, four or eight spored; ascospores are hyaline or dilutely colored, filiform, and non-septate.

The morophology of the genus is reexamined and the structure of the hysterothecium, the hymenium, the ascus, ascospores and paraphyses are described. Special attention was given to the position of the hysterothecium in the host tissue, the mycelial composition of the hysterothecium, the general structure of the hysterothecium and the nature of the slit. The mycelium, pycnidial forms, substomatal sclerotia and the development of the hysterothecium also received consideration. The author points out that the hysterothecium consists of two separate and distinct parts, the base and the cover which develop independently but simultaneously. In this character it differs from the apothecium of the Phacidiales or the perithecium of the Sphaeriales. On the basis of the mycelial type in cover and base and on the position of the hysterothecium in relation to the host tissues the author separates three genera from the current concept of Lophodermium, confining to that genus those species in which the hysterothecia are subepidermal and composed of pseudoparenchymatic tissues. Intra-epidermal hysterothecia of this type are segregated into a new genus Dermascia. The species with chitinized aliform plates forming the outer layers of the cover and the bottom layer of the base of the hysterothecium are placed in the genera Lophodermellina and Lophodermina of von Höhnel depending on their position in the host. The intra-epidermal forms are referred to the former, the subcuticular forms to the latter.

In the revised genus Lophodermium four new species, *L. acacicolum*, *L. Andropogonis*, *L. Miscanthi*, and *L. Phlei* are described. *L. Dactylis* is a new combination and *L. pinicolum* a new name proposed in the genus. In all 23 species are retained in the genus.

Dermascia is erected as a new genus with 14 recognized species of which *D. latispora* is the only one which is new. The others are transferred from Lophodermium.

Lophodermellina as set up consists of nine species of which one *L. Stevensii* is new. Three were placed here by von Höhnel and five are new combinations in this work.

Lophodermina comprises 24 species of which two, *L. prunicola* and *L. septata* are new and 20 were transferred into this genus by Tehon.

Eighteen species were excluded from the genus Lophodermium.

Two new genera of Hypodermataceae were erected to receive species which were not otherwise classifiable. *Epidermella* for *Hypoderma commune* Duby and *Lophodermium Lauri* Rehm and *Locelliderma* for *Hypoderma ampelodesmi* de Cesati.

The work reported in this treatment is carefully done and the rearrangement here proposed is a distinct advance over the former uncertainties of classification present in the Hysteriales.—JOSEPH C. GILMAN, Ames, Iowa.

THE LICHEN FLORA OF THE UNITED STATES, by Bruce Fink. Completed for publication by Joyce Hedrick. Ann Arbor: University of Michigan Press, 1935. 426 pp., 47 pls. $4.00.

Elaborating his "Lichens of Minnesota" (Contr. U. S. Nat. Herb. **14**, 1910) Professor Bruce Fink of Miami University at Oxford, Ohio, planned to write a comprehensive lichen flora of North America which was to supplant Tuckermann's entirely

antiquated "Synopsis of the North American Lichens" (1892). In 1922 he limited his project to the species occurring in the United States. During the next few years he not only studied personally the material of various American herbaria and determined that of numerous collectors, but he was assisted also by several outstanding European lichenologists, especially by E. A. Wainio and A. Zahlbruckner, who searched European herbaria for lichens from the U. S. and communicated to him the results of their studies. But the untimely death of Fink in 1927 terminated these investigations. Although the author had already assembled an extensive manuscript of specific diagnoses and prepared an approximate outline of the organization of the whole work, rich collections partly in European museums remained as yet undetermined and the revision of American species kept in these museums was discontinued, e.g. Zahlbruckner's work in Geneva in the herbarium of Müller Arg.

It seemed, therefore, that this monumental undertaking, the actual lifework of the author, would remain incomplete and unpublished; especially these works aiming at the highest possible degree of completeness remained in many instances incomplete through the death of the author, as Harmand's "Lichens de la France," Th. Fries' "Lichenographia Scandinavica"; and even Wainio's "Lichenographia Fennica," was completed only several years after the death of the author by B. Lynge.

It was, therefore, a highly meritorious task for which all lichenologists must be thankful that Mrs. J. Hedrick-Jones who had been Professor Fink's assistant for many years decided to prepare the manuscript for print, and to accomplish this in the best possible form according to the evident plans of the author. As introduction explaining mainly the morphology and anatomy of lichens that of Fink's earlier work "The Lichens of Minnesota" was retained in greater part. Moreover, keys to families and species had to be prepared. The systematic arrangement follows, with few minor deviations, A. Zahlbruckner's treatment in Engler-Prantl's "Natürlichen Pflanzenfamilien," 2nd ed. (1926). The specific diagnoses are brief and precise, containing only the characters decisive for the species. Detailed distribution records are unfortunately missing, only the State is given, while the extraterritorial distribution is not considered. The photographic habit figures of 47 pls. are excellent leaving nothing to be desired as regards plasticity and clearness. The drawings of anatomical details are taken mostly from Schneider's Textbook; they create an impression of ponderous unnaturalness.

A total of 1578 species and varieties are treated. Lack of completeness is accounted for by the history of the work. To produce something final is not given to man. Many new species will be discovered in this large territory; for instance, the Graphidaceae material from Florida, which the reviewer has undertaken to revise, is much richer in species than the treatment in this book indicates. But this fact should not hinder us from welcoming B. Fink's books as an important milestone in lichenology nor from gratefully acknowledging the great industry of this investigator. The best recommendation for a book is its necessity.—K. REDINGER, Vienna.

CHRONICA BOTANICA, an independent annual devoted to all branches of plant science, edited by Fr. Verdoorn. Leiden, Holland. Vol. I, 1935. 447 pp. 15 flor. holl.

This new venture, international in scope, is unique among botanical journals in being devoted to botanists and their activities. An introductory article by Dr. E. D. Merrill pleads for "international cooperation among botanists." An almanac follows, listing the most important dates in the history of botany. The rest of the book contains reports on the Sixth International Botanical Congress, other important congresses, meetings of societies, etc. The bulk of the volume consists of a "Review of all branches of plant science." This section, which is illustrated, contains most of the information that will be of immediate use to botanists. A section, reserved for letters to the editor, contains a variety of suggestions, and lists many current needs. There is a list of new periodicals as well as some advertisements. The publication of new and changed addresses will keep the International Botanical Address Book up to date. There is an index of personal names, names of plants, and of plant parasites. No botanist interested in more than his own work, should be without this volume.—TH. JUST.

REPRINT-SERIES

(Reprints 1, 2, 3 were issued with volume 2, reprint 4 with volume 3 and reprint 5 with volume 5).

(1) RAFINESQUE, C. S.—Neogenyton. 1825 ..... $ .25

(2) ———The Natural Family of Carexides. 1840 ..... .50

(3) ———Scadiography of 100 Genera of Ombelliferous Plants, etc. 1840 ..... 1.50

(4) ———Monographie des Coquilles Bivalves et Fluviatiles de la Rieviere Ohio. Remarques sur les Rapports Naturels des Genres Viscum, Samolus et Viburnum. A Bruxelles. 1820 1.50

(5) LECONTE, J. E.—Reprints of Monographs without plates 2.50
With 42 photographic copies of unpublished plates (7x8). ..... Prices on request

———Two extra plates reproduced from originals in New York Botanical Garden. ..... Prices on request

PUBLICATIONS

BAILEY, V.—Cave Life of Kentucky. 1933 ..... $ 1.25

FRIZZELL, D. L.—Terminology of Types. 1933 ..... .25

GREENE, E. L.—Pittonia. A Series of Papers Relating to Botany and Botanists. 5 volumes. 1887-1905 ..... 14.00

———Leaflets of Botanical Observation and Criticism. 2 volumes. 1903-12 ..... 6.00

———Manual of the Botany of the Region of San Francisco Bay. 1894. Bound cloth 2.00
Unbound 1.50

———Flora Franciscana. Parts I, II, III. (Part IV published long after the other parts, is quite unobtainable, as all copies not immediately distributed seem to have been lost in the San Francisco fire.) 1895. Price as published 2.00

———Cybele Columbiana. A Series of Studies in Botany, chiefly North American. (All published). 1914. ..... .75

The University of Notre Dame

Notre Dame, Indiana, U. S. A.

THE COLLEGE OF ARTS AND LETTERS

DEPARTMENTS

Religion
Philosophy
English
Classics
Modern Languages
History
Economics and Politics
Sociology
Journalism
Secondary Education
Physical Education
Art
Music
Speech

THE COLLEGE OF SCIENCE

DEPARTMENTS

Biology
Chemistry
Physics
Astronomy
Mathematics
Pharmacy

THE COLLEGE OF ENGINEERING

DEPARTMENTS

Civil Engineering
Mechanical Engineering
Electrical Engineering
Mechanical Drawing
Mining Engineering
Chemical Engineering
Architecture
Metallurgy

THE COLLEGE OF COMMERCE

DEPARTMENTS

Finance and Accounts
Foreign Commerce
Marketing and Business Administration

THE COLLEGE OF LAW
THE GRADUATE SCHOOL
THE SUMMER SESSION

The University of Notre Dame, the largest boarding school in the world, is located in northern Indiana adjacent to the industrial city of South Bend and eighty miles east of Chicago. There are two lakes on the 1,200 acre campus surrounded by beautiful groves, making an ideal setting for the pursuits of the scientist and naturalist.

For a Bulletin or other information, address

THE REGISTRAR - - Notre Dame, Indiana

The University Press, Notre Dame, Indiana